

# PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON

154th Session (1941-42)

Part 2

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PROCEEDINGS OF  
THE LINNEAN SOCIETY OF LONDON

154th Session (1941-2)

Part 2

PROCEEDINGS OF THE GENERAL MEETING

5 February 1942

Dr. E. S. RUSSELL, O.B.E., M.A., President,  
in the Chair

The Proceedings of the General Meeting held on Thursday, 27 November 1941, having been circulated, were taken as read and confirmed.

The PRESIDENT informed the Meeting that the Council recommend transference to the British Museum (Natural History) of the Collection of Birds' Eggs bequeathed to the Society in 1861 by John Drew Salmon, F.L.S., and asked for the Society's approval of this proposal.

The PRESIDENT drew attention of Fellows to the discussions that had been arranged for the present Session, particulars of which will be found in the notices.

The thanks of the Society were recorded for gifts made since the last meeting :—From Dr. R. Gurney, Mr. A. W. Haggis, Dr. Thomas Johnson, Professor F. E. Weiss, and Mr. Alain White.

Certificates of recommendation of the following candidates for Fellowship were read, for the first time in favour of Charles Earle Raven, D.D., Colonel William Percival Cosnahan Tenison, D.S.O., and Hitendra Kumar Baruah ; for the second time, in favour of Stella Ross-Craig (Mrs. J. R. Sealy) and William Glynn Burton.

A certificate of recommendation of the following candidate for Associateship was read for the first time, in favour of Willie Horace Thomas Tams.

The following communication was read and discussed :—

'The anatomy of the stem of palms and the problem of the artificial genus *Palmoxylon* Schenk.' By Mr. KAILAS NATH KAUL, F.L.S. (Discussed by the President, Mr. W. N. Edwards, Prof. F. E. Weiss, Dr. B. Barnes, Dr. C. R. Metcalfe, and Dr. J. Ramsbottom, O.B.E. ; Mr. Kaul replied.)

*Abstract.*—

Numerous works on the anatomy of the Palm-stems have already been published, because the characters of the Monocotyledons are most clearly exhibited in them, and they therefore afford the most favourable means of acquiring satisfactory ideas of the structure and growth of this great group of plants; but due to technical and other unavoidable difficulties the comparative anatomy of their stems has still remained very little understood. This problem has gained an extra importance by the fact that a large number of fossils undoubtedly belonging to this family have been discovered, and are being discovered, in the geological strata from the Cretaceous to the late Tertiary periods in the different parts of the globe. These remains are found in the form of leaf impressions or in the form of petrified material of fruits, seeds, inflorescences, roots and stems. Unfortunately, they are never found in organic connection to give us some clue to their systematic position in the family.

In the absence of satisfactory criteria for a natural classification palaeobotanists have been forced to group all this material into the artificial form-genera and species, as *Palmophyllum* sp. (palm leaves), *Palmocarpon* (palm fruits), *Rhizopalmoxylon* (palm roots), and *Palmoxylon* sp. (palm woods).

Obviously, in describing these forms and in giving them their proper natural position in our classification in vogue, which they so much deserve on account of the biological and geographical interest, it is necessary to establish relationship between the wood anatomy of modern species of palms with their leaves, flowers and fruits.

In 1888, F. H. Knowlton ('Description of two species of *Palmoxylon*—one new—from Louisiana', Proc. U.S. Nat. Mus. xi, p. 89; 1888), while describing two species of *Palmoxylon* from Louisiana, United States of America, wrote as follows:—'So little is at present known regarding the internal structure of the living species that it is only possible in the present state of our knowledge to mass together all the fossil species under the comprehensive generic name of "*Palmoxylon*", or simply "Palm-wood". It is true that the described species of *Palmoxylon* differ considerably among themselves, and it is more than probable that characters will ultimately be obtained that will allow of a separation into several generic types.'

In 1914 E. W. Berry ('Fruits of a Date Palm in the tertiary deposits of Eastern Texas', Amer. Journ. Sci. xxxvii, p. 403; 1914), while discussing the affinities of a date-like palm fruit from the tertiary deposits of Eastern Texas, wrote:—'There can be no doubt that these remains are those of a Phoenix-like fruit, and it is confidently expected that the foliage will eventually be discovered; in fact, some of the fragments of Palm rays found at this and other horizons in our southern Tertiary may represent this foliage. Petrified wood of several species of Palm is exceedingly abundant in these beds, while the study of Palm woods has not progressed to a point where one can speak with certainty of the generic relations of the petrified woods, it is significant that wood of several species occurs at this horizon.'

Thus the study of the stem anatomy of the modern Palm is absolutely essential to classify or identify this huge collection of *Palmoxyla*.



With this view, on the suggestion of Prof. B. Sahni who has been engaged on a comprehensive work ('Material for a Monograph of the Indian petrified Palms', Proc. Acad. Sci. United Provinces of Agra and Oudh, 1; 1931) on the Indian petrified palm-stems, the present study was undertaken and the anatomy of a large number of modern palm-stems was investigated. It was found as Mohl ('On the structure of the Palm Stem', eng. transl. Reports and Papers on Botany, Ray Society, London, 1849: German original, 1845) and Schoute ('Ueber das Dickenwachstum der Palmen', Ann. Jard. Bot. Buitenz. xi, p. 1; 1912) have already shown that Palm woods do not show any character of classificatory importance like bordered pits, resin canals or medullary rays, which have proved to be of great systematic importance in the Conifers. But at the same time it was found possible to establish generic forms on the appearance of the transverse sections of fully developed stems. It was found that the characters of the ground-tissue, which takes its definite form after the late secondary growth in thickness of the stem, are of great value for distinguishing natural genera of palms. Thus the definitive form of the ground tissue in *Phoenix*, *Chamaerops*, *Rhapis*, *Borassus*, *Caryota*, *Arenga*, is distinctive of these genera and is constant in all their species which show secondary growth in thickness. It is therefore possible to speak of a ground tissue of the *Borassus*-type, the *Arenga*-type and so forth. On the other hand, there are several characters, e.g. form of sclerenchyma, number and position of the fibro-vascular bundles, etc., which have served as a basis for various admittedly artificial schemes of classification (Unger, 'Plantae fossiles', Geschichte der Pflanzenwelt; Mohl, op. cit.; Stenzel, 'Fossil Palmenhölzer', Beiträge zur Paläontologie und Geologie, xvi, Heft iii & iv; 1904). These artificial characters, I find, may sometimes go hand in hand with the natural characters of the ground-tissue, but of course they cannot be used by themselves as safe guides for a natural classification.

Stenzel (1904) has already noticed that the structure of the ground-tissue is distinctive of the different species of fossil palms, but this feature could not be made use of by him in dealing with the fossil species because in the fossil material at his disposal specimens showing well-preserved ground-tissue in different parts of the same stem were rare. In the Indian material many species are available in which the ground-tissue characters of different parts of the same stem are well preserved.

By a detailed comparison of the living species with the extensive fossil material, which Professor Sahni has been describing in a monograph (not yet published), and which he kindly allowed me to compare for the present study, it has been found that *Palmoxydon coronatum* Sahni resembles the modern species *Borassus flabellifer* to such a great extent in all its anatomical characters, including the ground tissue, that I have no doubt that the fossil species is a species of *Borassus*. In this case even the peculiar corona-like growth of cells in the vascular parts of the dermal leaf-traces finds its counterpart in the modern form. So far as I know this anatomical feature has not been recorded in any other palm, living or extinct, except these two. The degree of resemblance is, indeed, so close (considering the form, size and distribution of the bundles and the position of the single big vessel in the fibro-vascular bundles) as to

raise the suspicion that *P. coronatum* may be the fossil form of the modern *Borassus flabellifer*; but, of course, this identity cannot be asserted without data concerning the floral characters. Between the fossil species *P. mathuri* Sahni and the modern *Bactris pallidispina* the resemblance extends to practically all the anatomical features. Thus they both have the same type of ground-tissue; the fibro-vascular bundles are more or less of the same type, and very small fibrous bundles are found uniformly distributed in the same manner in the lacunar ground-tissue in both the forms. It is therefore very probable that the fossil is a species of *Bactris*. Similarly, I believe that the fossil *P. sundaram* Sahni, which I find closely resembles *Cocos* in the form, size and distribution of the fibro-vascular bundles and specially in the ground-tissue characters, probably belongs to that genus.

There seems no doubt that more intensive and extensive comparisons between fossil and living palm stems will make it possible to refer many of the *Palmoxylo* to natural genera.

I wish to express my grateful thanks to the directors of the Royal Botanic Gardens, Calcutta, Peradeniya and Hakgala for allowing me to collect material of the palm stems from their Gardens and for giving me facilities in their Libraries and Herbaria. I am also highly indebted to Mr. Cotton and our late director, Sir Arthur Hill, for giving me help and protection during my present stay in this country. I wish to express my thanks to Mr. Atkinson, of our Kew Studio, for helping me in the preparation of the Chart and the slide. Finally, I wish to express my most sincere thanks to Mr. Edwards, of the British Museum, for lending the petrified stem of Palm and a section for demonstration this afternoon and for allowing me to work in his department.

#### *Discussion.*—

The PRESIDENT complimented Mr. Kaul and invited discussion.

Dr. C. R. METCALFE said that Mr. Kaul's paper clearly showed the value of the anatomical method in taxonomic work, and pointed out that a very useful purpose had been served in demonstrating which anatomical features are of most taxonomic value in the Palms, a group of plants which had received little recent attention from anatomists. The view was also expressed that more use should be made of the anatomical characters of the vegetative organs when studying the taxonomy of other groups of flowering plants. Attention was also called to the desirability for research workers to deposit a selection of their more important microscopical slides at some recognized institution for the study of systematic botany, so that their preparations would be available for use by future workers. A collection of microscopical slides for the study of systematic anatomy had been built up at Kew during the past 10 years, and it was hoped to extend this whenever opportunity permitted. It was pointed out that the excellent quality of Mr. Kaul's slides was not fully revealed in the projected illustrations of them which had been shown by means of the epidiascope during his lecture.

Read the following paper,—

'The later stages of Cleavage and the formation of the Primary Germ Layers in the Monotremata.' By Professor T. THOMSON FLYNN and



J. P. HILL, F.R.S. (Discussed by the President, Mr. I. H. Burkill; Dr. J. P. Hill replied.) [This paper will be published in the Transactions of the Zoological Society.]

Paper read in title,—‘A revision of the genera *Sphodromerus*, *Metromerus* and *Sphodronotus* (Orthoptera, Acrididae).’ By B. P. UVAROV, F.L.S. [Printed below.]

## A REVISION OF THE GENERA SPHODROMERUS, METROMERUS AND SPHODRONOTUS (ORTHOPTERA, ACRIDIDAE.)

By B. P. UVAROV, D.Sc., F.L.S., British Museum (Natural History).

(Plate 1 and 3 text-figures \*.)

*History of the Genera.*—The first species of the group was *Calliptamus serapis* Serville, 1838, on which Stål (1897) based his *Sphodromerus* as a subgenus of *Calliptamus*, while in 1875 he again merged it into the latter. Since then, a number of species have been described under *Sphodromerus*, but a critical revision has never been attempted. My notes (1922) on species of the genera *Sphodromerus* and *Kripa* were based on very scanty material and must be thoroughly revised. Chapman's (1937) discussion of North African species has a very restricted value, as he has considered only the Morocco-Algerian species, and even then omitted *S. cruentatus* Kr.

Kirby (1914) has erected the genus *Kripa* for an Indian species, but my subsequent study (1938) has proved it to be a synonym of *Sphodromerus*, while a closely allied genus, *Metromerus*, had to be erected to include *Caloptenus coelestiensis* G.-T., which for a time was in the genus *Kripa*.

One of the species described by me (1933) as *Sphodromerus cyclopterus* must now be removed to a new genus described below. *Sphodromerus inconspicuus* Schulthess (1894) does not belong to any of the genera under revision, as it is said to have flat fastigium of vertex and hind legs with a different type of pattern; its generic position in the group *Calliptamini* cannot be defined.

*Systematic position.*—The three genera comprised in the present study belong to the group *Calliptamini* of the subfamily Catantopinae, which is represented in the Palaearctic fauna also by the genus *Calliptamus*, from which they all differ by the male cercus having a single subapical tooth (two in *Calliptamus*) and by less regular and often practically obsolete lateral pronotal carinae. In the structure of the male cercus our three genera agree with *Caloptenopsis* I. Bolivar and *Acorypha* Krauss, of Africa and India, which both, however, have more or less specialized spurs of hind tibiae, while they are normal in our genera.

\* The cost of the reproduction of these illustrations has been borne by the Westwood Fund.

The inter-relations of the three genera under revision will be seen from the following key :—

- 1 (2). Middle femur on the outer side with only the upper furrow distinct (fig. 2 Sa). Hind femur very broad; upper carina strongly serrate; lower outer area distinctly widened behind the middle, with the lower carina usually serrate; pre-genicular constriction very distinct; outer genicular lobe short and broad (figs. 3 Se; 3 P; 3 Sa; 3 U). Fastigium of vertex narrower (figs. 1 U; 1 Se). Hind tibia with 6 (seldom 7) external spines. . . . . SPHODROMERUS St.
- 2 (1). Middle femur on the outer side with two furrows (fig. 2 C). Hind femur moderately broad; upper carina scarcely, or but finely, serrate; lower outer carina not widened behind the middle, with the lower carina smooth; pre-genicular constriction weak (fig. 3 C); outer genicular lobe elongate (fig. 2 C). Hind tibia with 9 (seldom 8) external spines. Fastigium of vertex broader (fig. 1 C).
- 3 (4). Pronotal disc weakly tectiform; lateral carinae weak and irregular, but distinct at least in prozona. Hind wings of normal shape . . . . . METROMERUS Uv.
- 4 (3). Pronotal disc strongly gibbose; lateral carinae absent. Hind wings very broad, strongly lobate externally (Plate 1, fig. 10) . . . . . SPHODRONOTUS, gen. nov.

*Ecology and distribution.*—Ecological information on members of this group is very scanty. In Palestine *Metromerus coelesyriensis* occurs commonly on bare soil of dry ravines, but is rare on the loamy plains near Jericho (Buxton and Uvarov, 1924). Both this species and *Sphodromerus sacer* are found, for example, in the Wady Kelt, a deep and intensely hot ravine with almost vertical rocky (limestone) sides, bearing sparse shrubby vegetation. Makarian (1930) says that *M. coelesyriensis* in Armenia is found only on hillocks with stony soil. Various species of *Sphodromerus* are all known only from more or less dry hilly areas with stony soil. This is the type of habitat commonly met with in the strongly eroded old mountain ranges on the northern fringe of the Eremian region, from the Anti-Atlas in Morocco, through the Saharan Atlas, Ahaggar, mountains of Tripolitania and Cyrenaica to Sinai, S. Palestine, Arabia, Iran and Baluchistan. A characteristic feature of this type of habitat is its discontinuity, which is reflected in a relatively large number of species of *Sphodromerus* due almost certainly to spacial isolation.

#### SPHODROMERUS Stål.

1873. *Sphodromerus* Stål, loc. cit. p. 72.—1875. *Sphodromerus* Stål, loc. cit. p. 12.—1902. *Sphodromerus* Martinez, loc. cit. p. 279.—1914. *Kripa* Kirby, loc. cit. pp. 195, 257.—1922. *Sphodromerus* Uvarov, loc. cit. pp. 118, 121.—1922. *Kripa* Uvarov, loc. cit. pp. 118, 124 (*partim*).

Genotype: *Calliptamus serapis* Serville, 1838 (by monotypy).

The number of species described under this genus, or referred to it, reaches 24, a large proportion of them being known from a few specimens, or even single types, while the descriptions are either lacking critical



comparison with other species, or made even more confusing by comparisons with doubtfully determined specimens. My observations on several species represented by good series of specimens tend to show that specific differences in this genus are often small and concern mainly the general habitus, comparative measurements of parts and details of coloration, particularly of the hind legs. Most of the differences of this kind cannot be gathered from descriptions, and this induced me to be very careful in synonymizing species not known to me by specimens. It is possible, therefore, that some of the 17 species with the additional 4 subspecies, may later prove to be either synonyms, or subspecies, of others, but this is a lesser evil than sinking a name without sufficient justification. On the other hand, most of the better known species appear to be very localized, and some new species and subspecies should be expected in the isolated mountain ranges of Northern Africa and South-Western Asia.

The key offered below is based on females, as the males of many species remain unknown, and it must be regarded as purely preliminary and artificial. The annotated list of species, following the key, includes only short descriptions of the less known species, without repeating the characters given in the key.

*Key to Species and Subspecies.*

- 1 (12). Fastigium of vertex narrow, deeply concave, its margins quite, or almost, straight, parallel (text-fig. 1 Se).
- 2 (11). Elytra normal, or slightly abbreviated, 2.4-3 times as long as pronotum. Hind wings not rose-coloured.
- 3 (6). Both elytra and wings with distinct oblique pre-apical fasciae (Plate 1, figs. 1 and 3).
- 4 (5). Elytra 2.7 times the length of pronotum, extending beyond hind knees; their apex obliquely rounded-truncate (Plate 1, fig. 1). Median pronotal carina low, obsolescent. Wings hyaline, pale violaceous basally; with a small pre-apical fascia in the first lobe, which is whitish apically. Hind femur relatively slender, 3 times as long as their maximum width (text-fig. 3 Se), bright sanguineous on the inside; inner knee-lobe and hind tibia on the inside of the same colour.—Sinai ..... 1. *serapis*.
- 5 (4). Elytra 2.5 times the length of pronotum, only reaching the hind knees; their apex parabolic (Plate 1, fig. 3). Median pronotal carina somewhat raised, sharp. Wings hyaline basally, infumate in more than the apical half, with a distinct, brownish pre-apical fascia and white apical edges of two first lobes. Hind femur short and broad, 2.4 times as long as its maximum width (as text-fig. 3 Sa), its inner face and the inner knee-lobe brownish-yellow, with an orange tinge; inside of hind tibia orange-yellow.—Hedjaz ..... 2. *arab*, sp. nov.
- 6 (3). Elytra not or weakly fasciated, or with the fasciae evenly distributed. Wings without a trace of a pre-apical fascia.

- 7 (8). Inside of hind femur, inner knee-lobe and hind tibia orange-yellow.—S. Algeria (Biskra) . . . 3. *decoloratus*.
- 8 (7). Inside of hind femur and hind tibia sanguineous.
- 9 (10). Elytra not abbreviated, 3 times as long as pronotum. Inner hind knee-lobe sanguineous. Size larger (female 39 mm., elytra 23 mm.).—E. Sahara (Oued Nsa) . . . 4. *cruentatus*.
- 10 (9). Elytra abbreviated, 2.4 times the length of pronotum. Inner hind knee-lobe yellow.—Morocco (Anti-Atlas) . . . 5. *occidentalis*.
- 11 (2). Elytra abbreviated, 1.4 times the length of pronotum (Plate 1, fig. 7). Hind wings light-rose.—S. Abyssinia . . . 6. *sanguiniferus*.
- 12 (1). Fastigium of vertex broader, shallower; its margins distinctly curved (text-fig. 1 U)
- 13 (34). Elytra normal, or slightly abbreviated, not less than 2.5 times the length of pronotum.
- 14 (15). Inside of hind femur, inner knee-lobe and hind tibia intense blackish-purple.—E. Palestine. 7. *sacer*.
- 15 (14). Inside of hind femur, knee-lobe and tibia not blackish-purple.
- 16 (27). Hind tibia with 6-7 spines on each side (not counting the inner apical spine). Hind femur short and broad, its length not more than 2.7 times its maximum width (text-fig. 3 P). Lateral pronotal carinae weak.
- 17 (24). Inside of hind femur with a very large black spot.
- 18 (23). Wings not bright-rose. Ovipositor normal.
- 19 (20). Elytra extending a little beyond hind knees, 3 times as long as pronotum, with distinct narrow pre-apical fasciae. Wings pale violet, with a weak pre-apical fascia. (Plate 1, fig. 2).—C. Sahara (Ahaggar Mts.) . . . 8. *tuarea*, **sp. nov.**
- 20 (19). Elytra not extending beyond hind knees, 2.7 times the length of pronotum; elytra and wings not or very weakly fasciated.
- 21 (22). Elytra scarcely narrowed to the apex. Wings hyaline. Lower inner sulcus of hind femur sepia-brown; hind tibia honey-yellow.—Cyrenaica . . . 9. *marmaricus*.
- 22 (21). Elytra distinctly narrowed to the apex, not fasciated, but with scattered spots (Plate 1, fig. 4). Wings pale violaceous basally. Lower inner sulcus of hind femur mahogany-red; hind tibia varying from clear yellow to orange-red.—SW. Arabia (Hadramaut) . . . 10. *pantherinus*.
- 23 (18). Wings bright rose. Lower valvae of the ovipositor unusually slender, strongly armed.—British Somaliland . . . 11. *calliptamoides*, **sp. nov.**
- 24 (17). Inside of hind femur without a black spot.
- 25 (26). Elytra 2.7 times the length of pronotum. Wings pale violaceous basally, with a weak pre-apical fascia. Inside of hind femur orange-red; inner knee-lobe and hind tibia orange-yellow.—S. Palestine . . . 12. *pilipes*.
- 26 (25). Elytra 3 times the length of pronotum. Wings light blue, or hyaline (var. *intermedia* Wern.). Inside of hind femur dark sanguineous; hind tibia light sanguineous.—Tripolitania . . . 13. *coerulans*.
- 27 (16). Hind tibia with 8 spines on each side (not counting the inner apical spine). Lateral pronotal carinae irregular, but distinct in the prozona.



- 28 (31). Inside of hind femur with a large black spot ; hind femur 2.8 times as long as its maximum width (text-fig. 3 U). Elytra not more than 2.8 times the length of pronotum.
- 29 (30). Elytra 2.8 times the length of pronotum, reaching the apex of hind knee, or slightly exceeding it. Wing hyaline, basally light rose.—Upper Baluchistan, N. Punjab . . . . . 16 a. *undulatus undulatus*.
- 30 (29). Elytra not more than twice the length of pronotum, only reaching the base of hind knee. Wing infumate in the anterior half, very faintly rose basally.—Punjab (Salt Range) . . . . . [sbsp. nov.]
- 31 (28). Inside of hind femur without a large black spot (at the most, dark brown at the base, the colour gradually fading posteriorly); hind femur at least 3 times as long as its maximum width. Wings long, hyaline, pale blue, or violet, basally. 16 b. *undulatus satinus*,
- 32 (33). Inside of hind femur, inner knee-lobe and hind tibia honey-yellow.—NW. and W. Central Iran . . . . . 17 a. *luteipes luteipes*.
- 33 (32). Inside of hind femur, inner knee-lobe and hind tibia red.—Lower Baluchistan (and N. Iran ?) . . . . . [sbsp. nov.]
- 34 (13). Elytra strongly abbreviated, not more than 1.5 times the length of pronotum. 17 b. *luteipes rubripes*,
- 35 (38). Wings rose, a little shorter than elytra. Hind tibia honey-yellow.
- 36 (37). Inside of hind femur with a large black spot. Hind tibia with 8 spines on each side.—N. India . . . . . [sbsp. nov.]
- 37 (36). Inside of hind femur without a black spot. Hind tibia with not more than 7 spines on each side.—Somaliland . . . . . 16 c. *undulatus pedestris*,
- 38 (35). Wings testaceous, minute (less than one-third of the length of elytra). 15. *somali*, sp. nov.
- 39 (40). Hind tibia, lower edge of the inner face of hind femur, and the inner part of its lower inner sulcus are blackish-purple; outer part of the sulcus sulphur-yellow.—Yemen . . . . . 14 a. *rathjensi rathjensi*.
- 40 (39). Hind tibia, inner face and the lower inner sulcus of hind femur are pale testaceous-yellow.—Yemen . . . . . [sbsp. nov.]
- 14 b. *rathjensi montanus*,

## 1. SPHODROMERUS SERAPIS (Serville, 1838).

(Plate 1, fig. 1; text-figs. 1 Se, 3 Se.)

1838. *Calliptamus serapis* Serville, loc. cit. p. 689.—1870. *Caloptenus scriptipennis* Walker, loc. cit. p. 686.—1876. *Calliptenus (Sphodromerus) serapis* Stål, loc. cit. p. 12.—1929. *Sphodromerus serapis* Innes Bey, loc. cit. p. 29.

*Description*.—Relatively large, rather robust. Frontal ridge with very obtuse margins and fine punctures, weakly narrowed under fastigium. Fastigium of vertex distinctly concave. Pronotal disc convex above, more so in prozona, which is smooth, while the metazona is densely, but weakly, rugulose; median carina very low, irregular, partly obsolescent; lateral carinae scarcely perceptible in prozona only. Prosternal tubercle conical, somewhat inclined forward. Mesosternal interspace in ♂ weakly, in ♀ decidedly transverse. Pre-apical fasciation of wings is weaker in the male.

*Notes.*—The type, if it still exists, was not available for study, but I have before me a well-preserved female from Sinai which I consider topotypical (see below), and a female and a male from Hedjaz. The Sinai female agrees perfectly with Serville's description, except for the coloration of the head, which was described as having 'chaperon largement bordé de noir luisant.' It is difficult to say what Serville meant by 'chaperon', but it was certainly not the epistome as translated by Martinez (1902, p. 280) : it was probably the upper edge of the antennal socket which in the female before me has a narrow black margin ; in a darker specimen the margin may well become broader.

Measurements of *Sphodromerus* spp. (in mm.).

|                                        | MALES. |            |         |             | FEMALES. |            |         |             |
|----------------------------------------|--------|------------|---------|-------------|----------|------------|---------|-------------|
|                                        | Body.  | Pro-notum. | Elytra. | Hind femur. | Body.    | Pro-notum. | Elytra. | Hind femur. |
| 1. <i>serapis</i> .....                | 27     | 7          | 20      | 16          | 38       | 9.5        | 28      | 23          |
| 2. <i>arab</i> .....                   | 22     | 5          | 14      | 13          | 34       | 9          | 20      | 19          |
| 3. <i>decoloratus</i> .....            | 24     | 6          | 17      | —           | 39       | 9          | 27      | —           |
| 4. <i>cruentatus</i> .....             | —      | —          | —       | —           | 39       | 7.5        | 23      | 18          |
| 5. <i>occidentalis</i> .....           | 22     | 5          | 12      | 11.5        | 31       | 7          | 18.2    | 18          |
| 6. <i>sanguiferus</i> .....            | 26     | 5.5        | 13      | 13          | 31       | 9          | 12.5    | 18          |
| 7. <i>sacer</i> .....                  | 28     | 6.5        | 15      | 15          | 32       | 8          | 20      | 18          |
| 8. <i>tuareg</i> .....                 | 26     | 6.5        | 19      | 16          | 40       | 10         | 28      | 22          |
| 9. <i>marmaricus</i> .....             | 20     | 5          | 13      | 11.5        | 31       | 7.3        | 18.5    | 17          |
| 10. <i>pantherinus</i> .....           | —      | —          | —       | —           | 38       | 9.5        | 24      | 20          |
| 11. <i>calliptamoides</i> .....        | —      | —          | —       | —           | 36       | 8          | 22      | 19          |
| 12. <i>pilipes</i> .....               | —      | —          | —       | —           | 35       | 9          | 23      | 21          |
| 13. <i>coerulans</i> .....             | —      | —          | —       | —           | 40       | 9          | 27.5    | 22          |
| 14. <i>rathjensi</i> .....             | —      | —          | —       | —           | 30       | 9          | 11      | 18          |
| 15. <i>somali</i> .....                | —      | —          | —       | —           | 31       | 7.5        | 12      | 16          |
| 16 a. <i>undulatus undulatus</i> ...   | 23     | 5.5        | 18      | 14          | 36       | 9          | 25      | 19          |
| 16 b. <i>undulatus salinus</i> .....   | 24     | 6          | 15      | 14          | 34       | 8.5        | 20      | 19          |
| 16 c. <i>undulatus pedestris</i> ..... | 23     | 6          | 16      | 14          | 30       | 8          | 11      | 18          |
| 17 a. <i>luteipes luteipes</i> .....   | 21     | 5          | 18.5    | 13          | 37       | 8          | 29      | 20          |
| 17 b. <i>luteipes rubripes</i> .....   | 23     | 6          | 19      | 13          | 40       | 9          | 32      | 22          |

As this was the first described species of *Sphodromerus*, the specific name *serapis* has been often misapplied to several other species, as will be seen later.

*Distribution.*—Serville's original description was based on a female brought from 'Egypt' by Bové, who has travelled, however, in Sinai as well as in Egypt. The species has never been re-discovered in Egypt, and Innes Bey's (1929) record from Solloum was based on my remarks about a specimen of *Sphodromerus* sp. (later proved to be *S. marmaricus* ; see under that species below). I believe, therefore, that the type locality for *S. serapis* was Sinai. The type of *Caloptenus scriptipennis* Walk. was from 'Wady Ferran, Arabia', which was probably Wady Feiran in Sinai. The species was recorded from Sinai between Wady Tarfa and the central mountains of the peninsula, by Krauss (1909, p. 35), and there is a female

from Fersh Arab, Sinai (*Kaiser*) in the British Museum. Other specimens in that Museum are from Arabia: Midian, 1 ♀; Umm al Salah, near Jidda, 14. xii. 1926, 1 ♂ (*Philby*). The species, therefore, appears to extend its area from Sinai along the Hedjaz coastal ranges at least as far south as Jidda. Literature record of *S. serapis* from Syria is due to the fact that Bolivar (1893) has reported it from the shores of the Dead



FIG. 1.—C=*Metromerus coelesyriensis*; U=*Sphodromerus undulatus*; Se=*S. serapis*. Vertex of female.

Sea, that is, from Palestine, in a paper dealing mainly with Syrian insects, and his determination, moreover, was incorrect (see below, under *S. sacer*, where other records from Palestine are also discussed). My own records from Iran (1912, 1914) were also incorrect (see under *S. luteipes* and *S. l. rubripes*).

## 2. SPHODROMERUS ARAB, sp. nov.

(Plate 1, fig. 3.)

*Description*.—Of medium size, moderately robust. Frontal ridge with obtuse margins and large punctures near the fastigium where it is very weakly narrowed. Fastigium of vertex strongly concave, with the margins almost sharp. Pronotum weakly tectiform; median carina sharp; lateral carinae in prozona weak but distinct, irregular, in metazona obsolete. Prosternal tubercle thick, conical. Mesosternal interspace decidedly transverse in both sexes. Preapical fascia of the wing distinct in both sexes.

*Notes*.—The characters given in the key and the smaller size distinguish this species from *S. serapis*. The somewhat abbreviated elytra make *S. arab* somewhat similar to *S. pantherinus*, which belongs, however, to a very different group according to the structure of fastigium and the unfasciated elytra and wings.

*Distribution*.—Arabia: Habala, ii. 1936, 2 ♀♀ (including the type); Khamis Mishait, vi. 1936, 1 ♂ (*Philby*; British Museum).

## 3. SPHODROMERUS DECOLORATUS Finot, 1894.

1894. *Sphodromerus decoloratus* Finot, loc. cit. p. xiii.—1896. *Sphodromerus decoloratus* Finot, loc. cit. p. 548.—1937. *Sphodromerus decoloratus* Chapman, loc. cit. p. 159, figs. 1, 2.

*Description*.—Detailed description was given by Finot (1895), while Chapman (1937) has supplied figures of the head, pronotum and hind femur.



*Notes*.—There is certainly a close affinity between this species and *S. serapis*, but their colour differences (see the key) are considerable. It is a matter for further study whether *S. decoloratus* is conspecific with *S. serapis*, but they certainly differ at least subspecifically.

*Distribution*.—Algeria : Biskra (*Finot*, loc. cit. ; also British Museum) ; Saida ? (*Finot*) ; El Kantara (*Burton* ; British Museum).

#### 4. SPHODROMERUS CRUENTATUS Krauss, 1902.

1902. *Sphodromerus cruentatus* Krauss, loc. cit. p. 247.

Described from a single female and not known to me by specimens, this species appears to be very close to *S. decoloratus* and to *S. occidentalis* while differing from both in the coloration of hind legs. It is not impossible that all three are only subspecies of one species.

*Distribution*.—S. Algeria : Oued Nsa (*Krauss*, loc. cit.). It is possible that the specimen from Laghouat mentioned by Chapman (1937, p. 159) also belonged to *S. cruentatus*, which that author has overlooked.

#### 5. SPHODROMERUS OCCIDENTALIS Chapman, 1937.

1937. *Sphodromerus occidentalis* Chapman, loc. cit. p. 157, figs. 1, 2.

*Description*.—See the original description and the key above.

*Notes*.—See under *S. cruentatus*.

*Distribution*.—French Morocco : Igherm, Anti-Atlas, about 5,800 ft. (*Chapman*, loc. cit.).

#### 6. SPHODROMERUS SANGUINIFERUS Rehn, 1901.

(Plate 1, fig. 7.)

1901. *Sphodromerus sanguiniferus* Rehn, loc. cit. p. 379.

*Description*.—Originally described from a single male, and I have before me a female which agrees well with the description except in the characters to be expected in that sex.

♀. Of medium size, robust. Frontal ridge with large punctures, very weakly narrowed under the fastigium. Fastigium of vertex relatively broad for the group, deeply concave, with the margins slightly convergent behind. Pronotum robust ; disc tectiform with the median carina well raised though irregular ; lateral carinae in prozona irregular but well distinct, in metazona perceptible only near the anterior margin. Prosternal tubercle broad at base, conical. Mesosternal interspace strongly transverse. General coloration ferrugineous, with numerous round blackish spots on head, pronotum and elytra. Wings light-rose, paler near the costal margin. Hind femur inside mahogany-red ; hind tibia yellow, with sanguineous tinge on the inside.

*Notes*.—Rehn did not mention the colour of hind wing in the type, probably because the specimen was not expanded. In the female sex the species is characterized by the strongly reduced elytra, in which respect, as well as in the coloration of the hind wing, *S. sanguiniferus* resembles *S. undulatus pedestris* and *S. somali*, differing from both in the structure of fastigium.

*Distribution*.—Described from an unrecorded locality in Southern Abyssinia or Italian Somaliland. The female in the British Museum is also from unknown locality in Somaliland (*W. Bury*).

7. *SPHODROMERUS SACER* (Giglio-Tos, 1893).

(Plate 1, fig. 6; text-figs. 2 Sa, 3 Sa.)

1893. *Caloptenus sacer* Giglio-Tos, loc. cit. p. 10, fig. 1.—1894. *Sphodromerus serapis* Giglio-Tos, loc. cit. p. 2 (*nec* Serville!).—1902. *Sphodromerus serapis* Martinez, loc. cit. p. 280 (*nec* Serville!).—1924. *Sphodromerus pilipes* Buxton and Uvarov loc. cit. p. 204 (*nec* Janson!).

*Description*.—Medium sized, but very robust. Frontal ridge broad, with large, though not deep punctures, gradually and very weakly narrowed under the fastigium. Fastigium of vertex broad, oval, very shallow. Pronotum very weakly convex above, disc matt, but not rugulose even in metazona: median carinae very low, but distinct;

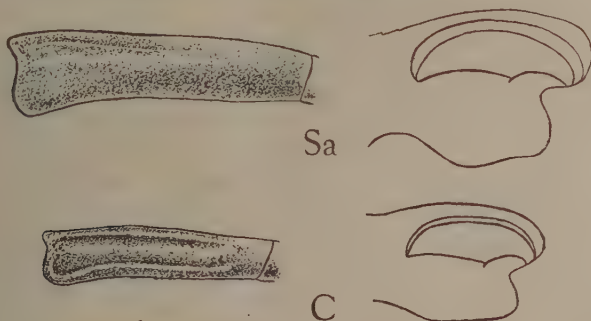


FIG. 2.—Sa=*Sphodromerus sacer*; C=*Metromerus coelesyriensis*.  
Right middle femur from outside, and left hind knee from outside.

lateral carinae in prozona practically straight, very obtuse, but distinct. Prosternal tubercle tapering weakly, almost cylindrical. Mesosternal interspace even in the female not, or scarcely, transverse. Elytra with very weak preapical fasciae: wings hyaline, with a light violaceous tinge near base, without apical fasciae.

*Notes*.—The topotypical specimens before me differ from the original description only in the coloration of the inner side of hind legs, which were probably discoloured in the type by preservation in fluid.

Giglio-Tos has himself (1894) made the mistake of synonymizing this strikingly distinct species with *S. serapis*, from which it differs abundantly in the general habitus, coloration, the structure of fastigium, width of hind femur (compare text-figs. 3 Se, and 3 Sa), etc. The description by Martinez (1902) was based on a female reported by Bolivar (1893) from the shores of the Dead Sea, as *S. serapis*, but clearly belonging to the present species.

*Distribution*.—E. Palestine: Jericho (*Giglio-Tos*, 1893); Jericho-Jerusalem, km. 24 (*Buxton*); Wady Kelt (*Buxton*); E. of Ramallah,

Wady Audsha (*Theodor*) ; E. of Hebron to Engeddi (*Theodor*). All these localities have been recorded on my determinations by Bodenheimer (1935) under *S. pilipes* which I then considered synonymous with *S. sacer* (see under *S. pilipes*).

### 8. SPHODROMERUS TUAREG, sp. nov.

(Plate 1, fig. 2.)

1934. *Sphodromerus decoloratus* Chopard, loc. cit. p. 115 (nec Finot!).—1937. *Sphodromerus decoloratus* Chapman, loc. cit. p. 158, figs. 1 and 2 (*partim* : nec Finot!).

*Description*.—One of the largest known species, moderately robust. Frontal ridge smooth, weakly narrowed under fastigium. Fastigium of vertex in male fairly deep and narrow, but in female shallow, broad and oval in shape. Pronotum very similar to that in *S. serapis*. Prosternal tubercle short and stout, weakly conical. Mesosternal interspace moderately transverse in both sexes.

*Notes*.—There is a considerable general resemblance between *S. tuareg* and *S. serapis*, but they are quite distinct in the structure of the fastigium, as well as in the coloration of hind legs. Chopard (1934), myself (1934) and Chapman (1937) have considered this insect as a form of *S. decoloratus*, but they belong to different groups by the structure of fastigium. The characters of *S. tuareg* are fairly constant in a very large series before me and its specific independence is difficult to dispute.

*Distribution*.—Algerian Sahara, Ahaggar mts. : Tirarat plateau, 5,800 ft., 23. ii. 1931, 2 ♂♂, 6 ♀♀, including the type ; Tin Giffuth, 7,500–7,700 ft., 2 ♂♂, 4 ♀♀ ; Ain Fergat, 7,300 ft., 4. iii. 1931, 1 ♂, 2 ♀♀ ; Ain Tabarir, 6,200 ft., 7. iii. 1931, 1 ♂ ; Tamsnigat, 6,900 ft., 3. iii. 1931, 1 ♀ ; 1 mile south of Tamsnigat, 6,900 ft., 26. ii. 1931, 1 ♀ (*Meinertzhagen* ; British Museum) ; Atakor-n-Ahaggar ; Oued Amsa ; In Fergane, 2,300 m. ; In Ameri ; Asekrem, 2,800 m. ; Ideles (*Chopard*, 1934). The British Museum series includes also several half-grown larvae from the same localities.

### 9. SPHODROMERUS MARMARIUS Capra, 1929.

1924. *Sphodromerus* sp. Uvarov, loc. cit. p. 39.—1929. *Sphodromerus marmarius* Capra, loc. cit. p. 146, figs. 13–18.

*Description*.—See Capra, 1929.

*Notes*.—A small and relatively short-winged species, recognized by its coloration.

*Distribution*.—Cyrenaica : Bardia (Capra, 1929) ; Egypt : Solloum (Uvarov, 1929 ; specimen in the British Museum).

### 10. SPHODROMERUS PANTHERINUS Krauss.

(Plate 1, fig. 4.)

1902. *Sphodromerus pantherinus* Krauss, loc. cit. p. 3.—1907. *Sphodromerus pantherinus* Krauss, loc. cit. p. 13, pl. i. fig. 8.

*Description*.—See Krauss, loc. cit.



*Notes.*—The abbreviated and spotted elytra, narrowing to the apex, as well as the coloration of hind legs, make this species abundantly distinct from all known ones. The male remains unknown, but has probably relatively longer elytra.

*Distribution.*—Arabia, Hadramaut: Makalla (*Krauss*, loc. cit.); limestone mts., north-west of Makalla, xi. 1935, 3 ♀♀ (*Maxwell-Darling*); Wady Humum (*Himim*), near Makalla, 9-10. v. 1931, 1 ♀; Shibam el Kaukaban, v. 1931, 1 ♀ (*Wissmann*); Wady Hadramaut, 1936, 2 ♀♀ (*Maxwell-Darling*).

The list of localities suggests that this species occurs on the barren Hadramaut hills, which come close to the coast at Makalla, but it will probably not be found in the coastal plain.

## 11. SPHODROMERUS CALLIPTAMOIDES, sp. nov.

*Description.*—♀. Frontal ridge more raised and with better defined lateral margins than in other species of the genus; its surface with fine scattered punctures. Fastigium of vertex moderately concave; rather wide; its margins practically straight. Pronotal disc weakly tectiform; median carina very distinct; lateral carinae irregular, but well distinct in prozona, and still perceptible in the anterior part of metazona. Prosternal tubercle short, conical. Mesosternal interspace transverse. Elytra reaching apex of hind knee, narrowed to a parabolic apex. Ovipositor slender, lower valvae strongly dentate. General coloration ochraceous; face and cheeks whitish; elytra with faint traces of dark oblique fasciae; wing hyaline, bright rose in the basal half, with blackish costa and other veins in the anterior part; hind femur on the inside mostly black, with a mahogany-red shade; its lower inner sulcus mahogany-red; hind tibia light red.

*Notes.*—The structure of the frontal ridge, the development of the lateral pronotal carinae, and the peculiar structure of the ovipositor, make it not improbable that this species may have to be removed from *Sphodromerus* when it becomes better known.

*Distribution.*—British Somaliland: Majojeh, Al Hills, 10° 54' N., 47° 12' E., 2,300 ft., 8. xi. 1929, 1 ♀ (*Colenette*).

## 12. SPHODROMERUS PILIPES (Janson, 1891).

(Text-fig. 3, P.)

1891. *Caloptenus pilipes* Janson, loc. cit. pp. 183, 185, fig. 4.—1924. *Sphodromerus pilipes* Buxton and Uvarov, loc. cit. p. 204 (*partim*).

*Description.*—Medium-sized, moderately robust. Frontal ridge with small and scattered punctures, weakly narrowed under the fastigium. Fastigium of vertex moderately broad, shallow, but with distinctly raised, practically straight, margins. Pronotum distinctly convex above, both in prozona and in metazona; disc rugulose in metazona; median carina distinct; lateral carinae in prozona irregular, weak. Prosternal tubercle short, conical. Mesosternal interspace in the female strongly transverse. Elytra and wings with pale, but distinct, pre-apical fasciae.

*Notes.*—The colour differences between this species and *S. sacer* have been summarized by me (Buxton and Uvarov, loc. cit.) when I incorrectly

regarded specimens from Wady Kelt as *S. pilipes*. The material of the true *S. sacer* received since leaves no doubt as to that species being well characterized (see above), and the single female type of *S. pilipes* differs from *S. sacer* not only in the coloration, but also in the narrower fastigium

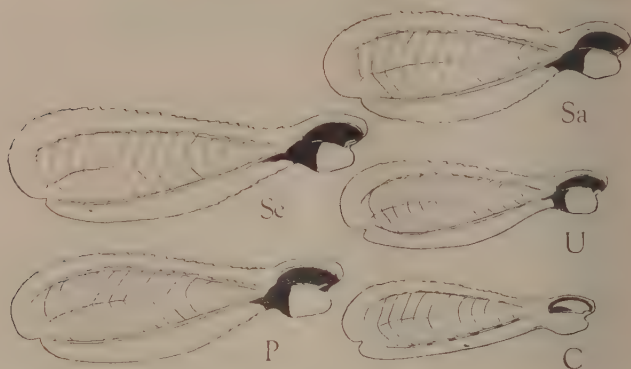


FIG. 3.—Se = *Sphodromerus serapis*; P = *S. pilipes*; Sa = *S. sacer*; U = *S. undulatus*; C = *Metromerus coelesyriensis*. Left hind femur from outside.

gibbose pronotum, broader and relatively longer elytra, and narrower hind femur. In most respects *S. pilipes* approaches *S. serapis* rather than *S. sacer*, but definitely differs from it by the wider fastigium.

*Distribution*.—Known only from the type taken in the Ghôr es Safieh, 1,250 ft. below the sea-level, at the south-eastern end of the Dead Sea.

### 13. SPHODROMERUS COERULANS Werner, 1908.

1908. *Sphodromerus coerulans* Werner, loc. cit. p. 716.—1908 a. *Sphodromerus coerulans* Werner, loc. cit. p. 127, pl. v. fig. 1.

*Description*.—See Werner, loc. cit.

*Notes*.—This species is known to me only from Werner's description and figure. The latter leaves no doubt that it must be referred to the group of species with the wide oval fastigium, while the coloration of its hind legs suggests a close similarity to *S. pilipes*.

Werner's (1908 a) var. *intermedia*, also unknown to me except by description, is said to differ by smaller size, unspotted head and pronotum and hyaline wings. Its status cannot be clarified without further study.

*Distribution*.—Tripolitania: Jebel Gosseba in the Gharian mts. south of Tripoli (Werner, loc. cit.).

### 14. SPHODROMERUS RATHJENSI RATHJENSI Uvarov, 1936.

(Plate 1, fig. 8.)

1936. *Sphodromerus rathjensi* Uvarov, loc. cit. p. 548.

*Description*.—See Uvarov, 1936.

*Notes*.—This species is unique in possessing quite rudimentary wings, and it is also well characterized by the strongly irregular lateral pronotal carinae. The typical subspecies is somewhat similar to *S. sacer* in the coloration of hind legs, but is abundantly different from it in the structure of pronotum.

*Distribution*.—Described from a single female taken at Sanaa, Yemen, about 7,900 ft., and known to me from four other females from the same locality (*Rathjens*; British Museum).

15 b. *SPHODROMERUS RATHJENSI* MONTANUS, *subsp. nov.*

*Description*.—Differs from the typical subspecies only in the coloration of hind legs as given in the key.

*Distribution*.—Yemen: Ghaiman, about 9 miles S. of Sanaa, Jebel Girwan, 9,200 ft., 17. ii. 1938, 1 ♀, type; foot of Jebel Kohl, about 15 miles N. of Sanaa, 9,000 ft., 1. ii. 1938, 1 ♀; summit of Jebel Kohl, 9,500 ft., 1. ii. 1938, 1 ♀ (*Scott and Britton*); Jebel Hada, 9,000 ft., 1 ♀ (*Dr. Petrie*).

This subspecies appears to replace the typical one on the higher volcanic hills rising on the Sanaa plateau, but further material and careful distribution studies are necessary to elucidate the inter-relation of the two forms.

15. *SPHODROMERUS SOMALI*, *sp. nov.*

*Description*.—Under medium size, moderately robust, with strongly abbreviated elytra and very broad and short hind femur. Frontal ridge weakly concave near the ocellus, not coarsely but rather densely punctured. Fastigium of vertex fairly broad, oval, shallowly concave, with well-raised margins. Pronotal disc tectiform, rugulose on metazona; median carina well raised; lateral carinae punctured and irregular in prozona, obsolete in metazona. Prosternal tubercle tongue-shaped, distinctly compressed in transverse direction. Mesosternal interspace transverse. Elytra reaching the middle of abdomen, strongly narrowed apically; wings as long as elytra. General coloration dark ochreous-brown; elytra blackish brown, with the apex whitish; wings rose, darkened apically; hind femur and tibia dirty-yellow.

*Notes*.—Similar to *S. sanguiniferus*, but differs well from it by the coloration of hind legs, by the elytral pattern and by the relatively shorter and broader hind femur.

*Distribution*.—Somali, 1 ♀ (*Miss Gillet*).

16 a. *SPHODROMERUS UNDULATUS UNDULATUS* Kirby, 1914.

1914. *Kripa undulata* Kirby, loc. cit. p. 257, fig. 137.—1933. *Sphodromerus undulatus* Uvarov, loc. cit. p. 380.

*Description*.—Kirby's original description and figure and my redescription contain the more important specific characters, to which the following (apart from those given in the key) should be added:

Fastigium in the female moderately wide, oval in shape, very shallow, with obtuse margins. Mesosternal interspace not transverse, even in the female. Pronotal disc weakly tectiform, finely and densely punctured; median carina distinct; lateral carinae in prozona distinct, but irregular.



The subsp. *undulatus* is characterized by the normally long elytra, while the other two subspecies have them reduced in a different degree. As already pointed out by me (1933), the female type from Campbellpur differs from other specimens by the light-red, instead of sanguineous, colour of hind tibia, but the taxonomic value of this character must remain uncertain until more material is available.

*Distribution*.—NW. Punjab : Campbellpur (*Kirby*, loc. cit.); Sind : Shah Hussan. Upper Baluchistan : Harnai ; Ziarat : Chatair ; Sharigh (various collectors).

This subspecies appears to be distributed mainly in the hilly parts of Baluchistan, with outlying occurrences in NW. Punjab and Western Sind.

16 b. *SPHODROMERUS UNDULATUS SALINUS*, subsp. nov.

*Description*.—Differs from the typical subspecies only in a reduction of elytra and infumation of wings, while the rose colour of the latter is very faint, especially in the male.

*Distribution*.—Punjab : Sakesai, Salt Range, 3,500 ft., 19–21. iv. 1931. 2 ♀♀, including the type (*Pruthi*) : Khewra, Salt Range, 24. ix.–x. 30. 2 ♂♂ (*Hora and Pruthi*). Type in the Indian Museum, Calcutta ; a pair of paratypes in the British Museum.

This race appears to be restricted to the isolated Salt Range mountains of the Punjab.

16 c. *SPHODROMERUS UNDULATUS PEDESTRIS*, subsp. nov.

(Plate 1, fig. 9.)

*Description*.—The female is quite brachypterous, with intensely coloured rose wings, while the male elytra reach the base of hind knee and the wings are strongly infumate throughout, sometimes losing all trace of rose colour.

*Distribution*.—N. Punjab : Dhar, Murree division, 5,000 ft., 20. ix. 28. 3 ♀♀, including the type (*Pruthi*). Chitral : Ramram Gol near its junction with the Chitral river, below Arandu, 15–16. ix. 29, 1 ♂ ; between Tar an Drosh, 6–10. x. 29, 2 ♂♂ (*Chopra*). Type in the Indian Museum, Calcutta ; a pair of paratypes in the British Museum.

Probably proper only to higher altitudes in NW. India.

17 a. *SPHODROMERUS LUTEIPES LUTEIPES* Uvarov, 1933.

1933. *Sphodromerus luteipes* Uvarov, loc. cit. p. 228.

*Description*.—The male has been fully described by me. In the female the fastigium is moderately broad, oval, concave ; mesosternal interspace almost square.

*Distribution*.—W. Iran : Isfahan ; Simnan ; Damghan (*Uvarov*, 1933).

17 b. *SPHODROMERUS LUTEIPES RUBRIPES*, subsp. nov.

(Plate 1, fig. 5.)

*Description*.—Differs from the typical subspecies only by the red coloration of hind legs. In the male sex there is a tendency to a darkening

of the inside of hind femur, so that a resemblance to *S. undulatus* is obtained, but wings are of different colour.

*Distribution*.—Lower Baluchistan (Mekran) : Punjgur, 1 ♂, 1 ♀, type ; Kunak, 1 ♀ ; Buleda, 1 ♀ ; Patkin, 1 ♀ ; Saidan, 1 ♀ ; Pidark, 1 ♀ ; Pasni, 2 ♀♀ ; Tump, 1 ♂ (various collectors of the Indian Locust Research organization).

I refer to this subspecies, with some hesitation, a specimen from Kopet Dagh in Northern Iran, between Gaudan and Kutshan, incorrectly recorded by me (1912) as *Sphodromerus serapis*. It has been sent to me recently by Mr. Mistshenko, as a paratype of *S. luteipes ornatus* Mistsh., but I am not aware that this name has ever been published. In the latter case, my subsp. *rubripes* will have to be regarded as a synonym of *ornatus*.

### METROMERUS Uvarov, 1938.

1922 a. *Kripa* Uvarov, loc. cit. p. 124 (*partim, nec Kirby* !).—1928. *Metromerus* Uvarov, loc. cit. p. 379.

Genotype : *Caloptenus coelesyriensis* Giglio-Tos, 1893.

The original description and the characters given in the key to genera above should be sufficient to recognize this genus.

The genus includes one species, somewhat variable geographically but with only one clearly defined subspecies.

#### 1. METROMERUS COELESYRIENSIS (Giglio-Tos, 1893).

(Text-figs. 1 C ; 2 C ; 3 C.)

1893. *Caloptenus coelesyriensis* Giglio-Tos, loc. cit. p. 10, fig. 4.—1902. *Caloptenus coelesyriensis* Martinez, loc. cit. p. 296.—1914. *Calliptamus italicus* ab. *carbonaria* Uvarov, loc. cit. p. 226.—1922. *Sphodromerus coelesyriensis* Uvarov, loc. cit. p. 366, fig. 2 A.—1922 a. *Kripa coelesyriensis* Uvarov, loc. cit. p. 125, pl. i, fig. 2.

*Notes*.—The area of the specific distribution is a wide one (see below), but it is discontinuous, as the species has special ecological requirements. It is natural, therefore, to expect a considerable variation in the populations from different areas, and this is actually observed. Thus, specimens from Central Iran are relatively more slender, with longer elytra than those from Palestine and Transcaucasia. The only Syrian (*i. e.*, topotypical) male before me is relatively large, with very broad fastigium of vertex, while in all others the fastigium is somewhat narrower though not as narrow as in the subsp. *angusta*. It would be, however, inadvisable to attempt defining different subspecies until more material can be studied, and subsp. *angusta* is the only one that can be recognized at present.

*Distribution*.—Definitely known from Palestine, Syria, SE. Turkey (Urfa, British Museum) ; Armenia (Erivan, Ordubad), N. Iran (Ramme, Eos, v. 1929, p. 159), C. Iran (Tehran, Isfahan, Nishovar ; British Museum) ; Turkestan (Uvarov, 1914). My record from Siwa in Egypt (Uvarov, 1929, p. 39) was based on a larva and needs confirmation.

1a. *METROMERUS COELESYRIENSIS ANGUSTA* (Uvarov, 1934).1934a. *Kripa coelesyriensis angusta* Uvarov, loc. cit. p. 118, fig. 38a*Notes*.—The differences of this subspecies from the typical one were given in the original description.*Distribution*.—Turkey : Ankara (Uvarov, loc. cit.).**SPHODRONOTUS, gen. nov.**

As can be seen above, from the key to the genera, *Sphodronotus* represents distinct specialization in the structure of pronotum as well as in the shape of hind wings. In its general habitus it is nearer to *Sphodromerus* than to *Metromerus*, but agrees with the latter in the structure of both middle and hind femora, as well as in the armature of the hind tibiae.

Genotype : *Sphodromerus cyclopterus* Uvarov, 1933.1. *SPHODRONOTUS CYCLOPTERUS* (Uvarov, 1933).

(Plate 1, fig. 10.)

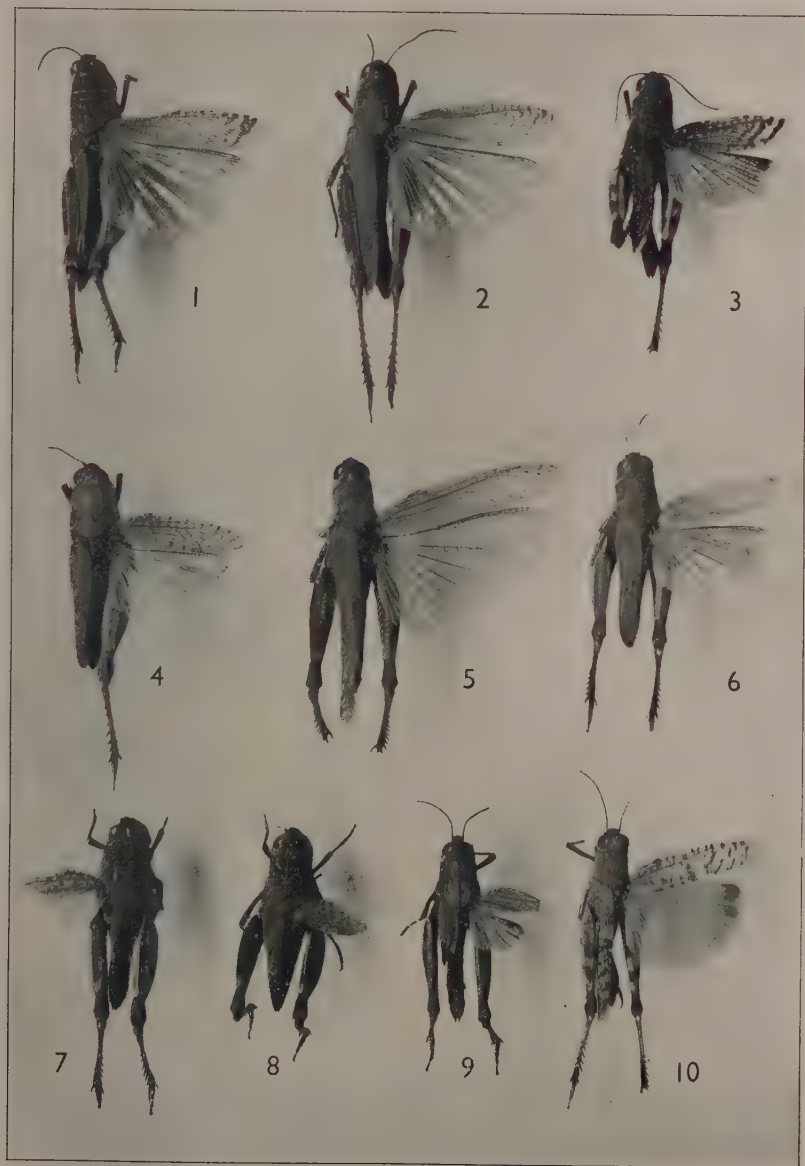
1933. *Sphodromerus cyclopterus* Uvarov, loc. cit. p. 227.*Description*.—See Uvarov, loc. cit.*Distribution*.—Known only from Southern Iran : Disful in Arabistan ; Masjid-i-Sulaiman, N. of Ahwaz (Uvarov, loc. cit.).

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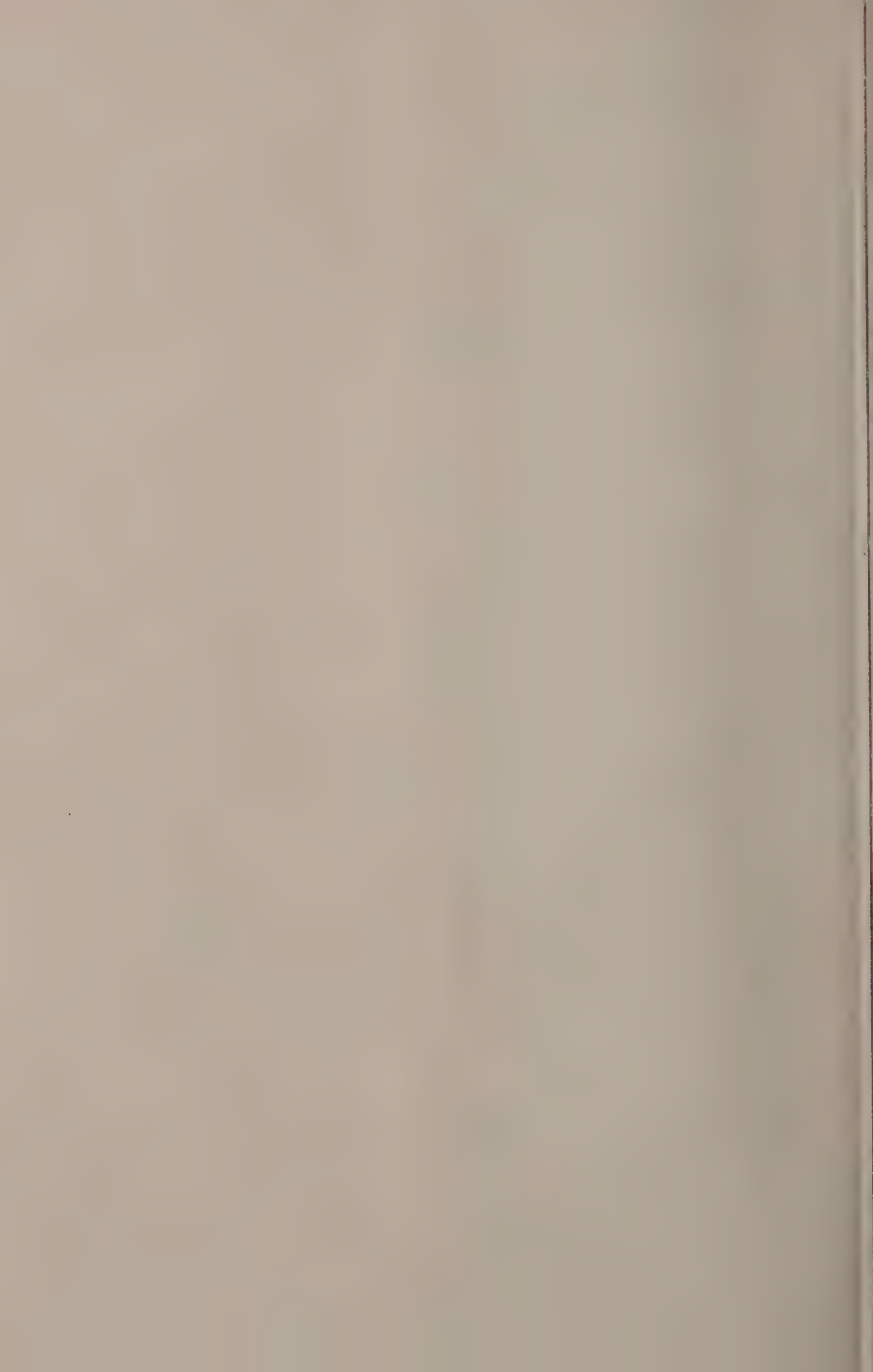
[In every case, the reference is given to the actual pages of a paper where the species of the group under revision are discussed.]

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## EXPLANATION OF PLATE 1.

- Fig. 1. *Sphodromerus serapis* (Serv.), ♀. Sinai.
- Fig. 2. *Sphodromerus tuareg*, sp. n., ♀, paratype. Ahaggar mts.
- Fig. 3. *Sphodromerus arab*, sp. n., ♀, paratype. Arabia.
- Fig. 4. *Sphodromerus pantherinus* Kr., ♀. Hadramaut.
- Fig. 5. *Sphodromerus luteipes rubripes*, subsp. n., ♀. Baluchistan.
- Fig. 6. *Sphodromerus sacer* (G.-T.), 1 ♀. Jericho.
- Fig. 7. *Sphodromerus sanguiferus* Rehn, ♀. Somaliland.
- Fig. 8. *Sphodromerus rathjensi* Uv., ♀, paratype. Yemen.
- Fig. 9. *Sphodromerus undulatus pedestris*, subsp. n., ♀. Punjab.
- Fig. 10. *Sphodronotus cyclopterus* (Uv.), ♂, paratype. SW. Iran.



PROCEEDINGS OF THE GENERAL MEETING  
19 February 1942

Dr. E. S. RUSSELL, O.B.E., M.A., President,  
in the Chair

The Proceedings of the General Meeting held on Thursday, 5 February 1942, having been circulated, were taken as read and confirmed.

The thanks of the Society were recorded for a gift made since the last meeting :—From Professor F. E. Weiss.

Certificates of recommendation of the following candidates for Fellowship were read, for the second time in favour of Charles Earle Raven, D.D., Colonel William Percival Cosnahan Tenison, D.S.O., and Hitendra Kumar Baruah ; for the first time, in favour of Elizabeth Alice Flint.

A certificate of recommendation of the following candidate for Associateship was read for the second time, in favour of Willie Horace Thomas Tams.

The President reported the deaths of the following Fellows :—Mr. Arthur Grove and Mr. J. J. Sheldon.

The following communication was read and discussed :—

Dr. C. B. WILLIAMS. The Migration of Butterflies. (Discussed by the President, Mr. Cecil H. Hooper, Dr. L. Richmond Wheeler, Mr. I. H. Burkill, Dr. Malcolm Smith and Dr. R. Melville ; Dr. Williams replied.)

*Abstract.*—

Dr. WILLIAMS gave a general survey of our present knowledge of the problem of migration in the Lepidoptera. He first outlined the movements of the three best known butterfly migrants, the Monarch (*Danaus plexippus*), the Painted Lady (*Vanessa cardui*) and the Cabbage White (*Pieris brassicae*). He then discussed problems arising from the facts, such as orientation, the question of the return flight, and the relation between flight of the same insect in different areas, and different insects in the same area. On the question of orientation it was shown to be very unlikely that the direction of the wind had anything but a minor effect on the direction of the flight ; and it was pointed out that evidence of a return flight (often in quite small numbers) had been found recently in a number of species in which it had been previously unsuspected. Evidence has also brought forward that migrations of the Painted Lady Butterfly and the Hawk Moth, *Celerio lineata*, tend to occur simultaneously on both sides of the Atlantic. It was also possible by the results of recent research to group the British migrant butterflies and moths into several classes the members of which tend to occur in numbers simultaneously, but are negatively correlated with members of other groups.

An account of the main points of the lecture has been published in the Transactions of the Royal Entomological Society, xcii, pp. 101-282; 1942.

*Discussion :—*

Mr. CECIL H. HOOPER asked : Is the Small Tortoiseshell butterfly found to be one of the most constant butterflies to pass the winter in England ? Is it a fact that Orange Tip butterflies are more abundant each seventh year ? Then he added that a great number of Cabbage butterflies winter in England in the chrysalis state, and that at the same time it is occasionally recorded that ships in the Channel come into a cloud of Cabbage butterflies crossing from France to England, the insects even so numerous that they considerably obscure the light.

Dr. L. RICHMOND WHEELER said that many interesting examples had been given and he did not wish to be a wet blanket, but in some countries, in Malaya at least, definite migrations of butterflies were very rare ; yet over 900 species were found there and some were common.

But minor, daily movements, up and down sunny hillsides, for example, often occurred ; in these the butterflies did not seem to get any ' forrader.' He enquired whether Dr. Williams considered such movements to be of a migratory character.

Mr. I. H. BURKILL said that he had never seen a butterfly migration in Malaya, but had in India, and on the request of Dr. Williams undertook to look up an entry \* he had made in his diary. He described the flight as a spaced out procession, adding that the spacing excluded the possibility of all the insects taking direction from each other.

Dr. MALCOLM SMITH asked how far butterflies could travel over the sea. The only migration he had seen was in Cambodia. It was an extensive migration and was travelling almost due south. The nearest land in that direction was Borneo, about 500 miles away.

In reply, Dr. WILLIAMS stated :—

(1) That while migratory flights appear to be common in East Africa, Ceylon and parts of India, there were very few records from Malaya.

(2) That migrating butterflies regularly cross open water in places, such as the Mediterranean, where it might be several hundred miles wide.

(3) That there is little evidence that the butterflies in flight take their direction from one another ; flights are frequently so thin that the butterflies are well out of sight of one another.

Read the following two papers,—

Dr. B. BARNES, F.L.S. Abnormal seedlings of the pimpernel (*Anagallis arvensis* Linn.). (Discussed by Prof. F. E. Weiss ; Dr. Barnes replied.) [Printed in full, p. 88.]

WILLIAM GREENWOOD. The adventive and weed flora of the leeward coasts of Fiji. (Communicated by the late Sir ARTHUR W. HILL, F.L.S.) (Read by the BOTANICAL SECRETARY, and discussed by Dr. L. Richmond Wheeler and Mr. Cecil H. Hooper ; Mr. Burkill replied.). [Printed in full, p. 92.]

\* Entry, made on 30 October, 1902, at the Chharodi Cattle Farm, which is 22 miles north-west of Ahmedabad, with grass lands to the west but cultivation to the east :—  
' Innumerable butterflies were flying over the grass in a north-easterly direction, half against the prevailing wind and half across it. They were almost all of a white species and they never settled.'

SEEDLING ABNORMALITIES IN *ANAGALLIS ARVENSIS* LINN.

By B. BARNES.

EARLY in May 1935, many seedlings of *Anagallis arvensis* appeared in my garden from self-sown seeds ripened in the previous autumn. After some tricotylys were noticed among them, it seemed worth while to go over the whole of the plants in order to determine the frequency of tricotyly in this non-selected population. Accordingly, all were dug up and put aside in a preservative fluid. Later, each seedling was inspected, and, as a result, the table below was compiled.

TABLE I.

Composition of a wild population of seedlings of *Anagallis arvensis*.

| Number of cotyledons. | Form of cotyledons.        | Condition of first whorl of foliage leaves. | Number of seedlings showing the characters. |
|-----------------------|----------------------------|---------------------------------------------|---------------------------------------------|
| 2                     | Normal.                    | 2-membered.                                 | 1138                                        |
| 2                     | { One normal, one lobed. } | 2-membered.                                 | 2                                           |
| 2                     | { Both deeply lobed. }     | 2-membered.                                 | 1                                           |
| 3                     | Normal.                    | 2-membered.                                 | 18                                          |
| 3                     | Normal.                    | 3-membered.                                 | 13                                          |
| 3                     | { Two normal, one lobed. } | 2-membered.                                 | 1                                           |
| 3                     | Normal.                    | { 3-membered, but leaves united. }          | 1                                           |
|                       |                            |                                             | Total 1174                                  |

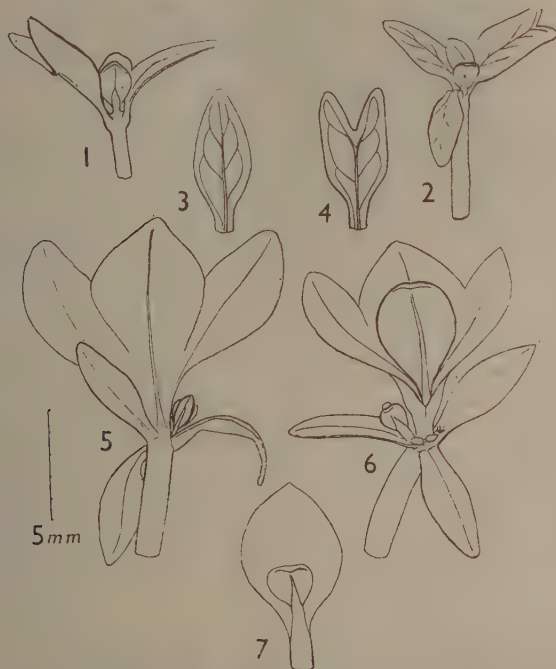
The population contained small numbers of types other than straight-forward dicotylys and tricotylys. Even though observations have been limited to the gross external features of the seedlings, they have provided a few points which seem to merit a short description.

Very few of the young plants had gone beyond the production of the first whorl of foliage leaves, and these leaves were mostly small and immature. As all the seedlings had begun to form the first whorl of leaves, it is probable that the cotyledons had reached their final shape, if not their full size, when the plants were gathered. In all but fourteen of the seedlings, the first whorl of ordinary leaves was two-membered. The fourteen exceptional plants were part of the thirty-three tricotylys found in the population; thirteen had a three-membered first whorl of foliage leaves; in the fourteenth plant, although the first whorl consisted of three leaves, these leaves were united by their petioles and laminas, giving a peculiar condition to be described more fully below.

The cotyledons of most of the tricotylys did not differ in any significant respect from those of the normal dicotylys. The middle lines of these cotyledons diverged very regularly at angles of  $120^\circ$ , giving a neat,



symmetrical effect when viewed from above; this regularity was not so obvious in the tricotyl which had one lobed cotyledon. The tricotyts had at least one-third more assimilating tissue than had the dicotyts, and yet it was noticeable that most of them were slightly behind the dicotyts in development. I have seen comparable conditions in dicotylous and tricotylous seedlings of *Antirrhinum majus*. It remains to be determined



FIGS. 1-7.—*Anagallis arvensis* Linn. Abnormalities in seedlings.—1. A dicotyl with one normal and one lobed cotyledon. 2. A tricotyl with two normal cotyledons and one lobed cotyledon. 3. A normal cotyledon, dorsal surface. 4. A lobed cotyledon, dorsal surface. 5-7. The tricotyl with fused epicotyledonary leaves. 5 and 6. Views from opposite sides. 7. The pair of unequal leaves which followed the epicotyledonary whorl. All the figures are drawn to the same scale, which is indicated on the left of the figures.

if the lag is because seeds which yield tricotyts germinate more slowly than those which give dicotyts, or if tricotyts are less vigorous than dicotyts; I suspect the latter, but tests are needed to settle the point.

The population included four seedlings with lobed cotyledons; two dicotyts each with one-lobed cotyledon (fig. 1), one dicotyl with both cotyledons lobed, and one tricotyl with two entire and one lobed cotyledon (fig. 2). It seems preferable to regard these cotyledons as lobed rather than as split (*i. e.*, schizocotyts), for there is no way of deciding how they developed in their early stages.

When a lobed cotyledon was borne in company with one or two normal cotyledons, it was of about the same length, and the same maximum width as its companions, and its petiole seemed to be quite ordinary. The apical sinus did not reach half-way along the leaf, and in some was even more shallow. The apex of the sinus had a thickened rim, which appeared to be a local thickening of the margin, projecting on the dorsal side of the cotyledon. The venation agreed with that of a normal cotyledon, except that the middle vein ended abruptly a little short of the sinus, and sent one strong lateral vein into each lobe: it agreed in general with the venation figured by Turnbull (Ann. Bot. III, p. 127; 1889) for the normal lobed cotyledons of *Convolvulus*.

At first the dicotyl with two lobed cotyledons was taken for a tetra-cotyl, but there were only two cotyledonary petioles, each bearing a bilobed lamina divided as far as the distal end of the petiole. Except for the deeper lobing, these cotyledons agreed in shape with the less deeply lobed cotyledons (fig. 4). Each lobe was almost a parallelogram, with angles of approximately  $150^{\circ}$  and  $30^{\circ}$ , and was inserted on the petiole by one of its acute angles. The venation in each lobe corresponded to that of a whole cotyledon (fig. 3), but the main vein was not truly median. It lay over towards the sinus. The lateral veins on each side anastomosed in the usual manner.

It remains to describe the very peculiar seedling which has been mentioned: it is represented in figs. 5, 6 and 7. It was the largest of all the seedlings collected. The cotyledons were normal for an ordinary tricotyl. Each subtended a bud, and each of these buds had produced a branch bearing a pair of foliage leaves, still very small. The formation of branches from buds in the axils of cotyledons is common in the seedlings of *Anagallis arvensis*, but whereas development is usually of equal strength from the two or three buds of that group, in this seedling one bud had produced a much stronger branch than had either of the others, stronger, indeed, than any of the corresponding branches of any other seedling of the gathering.

The foliage leaves on the main shoot of the seedling provided the chief point of interest. The first whorl was three-membered, but the petioles of these leaves were extended laterally, and united below to form a short, asymmetrical pouch, open nearly to the base on one side. On the opposing side, there was union not only of the petioles, but also of the laminas of the leaves for some two-thirds of their length. A short length of the main axis arose from the bottom of the pouch, bearing terminally a pair of leaves, one being much larger than the other. The small leaf lay opposite to the midrib of the middle member of the three joined leaves of the whorl below, while the larger leaf occupied most of the gap where the laminas of those leaves had not joined.

In this seedling the change from a three-membered to a two-membered whorl occurred between the first and second whorls of foliage leaves on the main axis, and between the cotyledons and the first whorls of leaves on the lateral axes. In eighteen of the ordinary tricotyls, the change occurred between the cotyledons and the first leaves on the main stem. The difference in the size of the two members of the first whorl suggests that even at that level a balance had not been attained, for it is unusual

in *Anagallis arvensis* for the two leaves of a pair to differ much in size. Altogether, this seedling seems to have been in an unbalanced state, and it is regrettable that its special features were not recognized when it was alive, for it might have proved interesting to have grown it to maturity.

The anatomy of these seedlings has not yet been studied. The absence of anatomical data makes unprofitable an attempt to link up with the work of the several investigators who have discussed the anatomy of seedlings in relation to aberrations in their external form. The seedlings which have been briefly described here grew from seeds produced from apparently normal plants in ordinary garden soil, and without any special treatment. It may be that the fairly high (but undetermined) lime content of the soil had had an effect, for *Anagallis arvensis* is said to be somewhat lime-shy, but this is no more than a guess. An explanation based on a conjectured injury to a growing point does not seem very acceptable. Injury might explain the abnormalities of the foliage leaves of the particularly abnormal seedling, but it is difficult to use the suggestion to explain tricotyly when this is indicated by symmetrically-placed and seemingly quite healthy cotyledons, each subtending a normal bud. The emphasis which, rightly, has been placed on the importance of dicotyly in the flowering plants, seems to have engendered a reluctance to admit that meristic variation may affect even this deep-seated character, and to have favoured explanations based on suggestions of injury to growing points or of the splitting of rudiments. The latter explanation, taken to its limits, would seem to merge into meristic variation, but by using it, the need is avoided of supposing that the fundamental dimery has been disturbed. When, however, apparently healthy tricotylys with cotyledons all of the same size and symmetrically disposed are considered, it is not easy to agree that there has been a splitting somewhere in the ontogeny of one or more of the cotyledons. It seems much more likely that their rudiments arose and developed independently. This explanation is not so satisfactory when applied to the lobed cotyledons, but these may as well be explained by supposing that the rudiments have fused as that they have split.

If subsequent work shows that the dicotylys are more vigorous than the tricotylys—and this is very probably true of *Antirrhinum majus* if not of *Anagallis arvensis*—there will here be an indication that the dicotylys are better balanced in general organization than are the tricotylys, and that the success of a seedling is not necessarily conditioned by the area of its assimilating tissue. On theoretical grounds it would seem that the greater the assimilating surface, the better the chance of the seedling surviving what is probably the most critical phase in the life of a plant, that of establishment, and this leads to the speculation that the occurrence of tricotyly in many families of dicotyledons, not all closely related, may be an experiment in evolution, which, if it succeeds, will make dicotyly a less important character than it now is.

#### *Discussion :—*

Professor WEISS expressed his interest in Dr. Barnes's communication and enquired whether some of the seedlings which showed three-membered



whorls of leaves retained these in the later branches or went back to two-membered nodes, also whether the plants with two-membered whorls subsequently developed three-membered whorls. He had often observed in adult plants both two- and three-membered whorls in the mature plants varying with the vigour of the plants.

In his reply Dr. BARNES stated that the plants had not been grown on to maturity.

## THE ADVENTIVE AND WEED FLORA OF THE LEEWARD COASTS OF FIJI.

BY WILLIAM GREENWOOD.

THE two largest islands of the Fiji group are Viti Levu and Vanua Levu. Along their leeward coasts sugar production is the main agricultural pursuit. It is prosecuted over about 140 miles of coast line in Viti Levu, chiefly near rivers and creeks which intersect the low land, and in the numerous small valleys running into the hills. In some places the hills run out to the sea, breaking the continuity of the flat coastal strip. This strip is so narrow that were it not for the valleys the cane-growing area would extend nowhere more than three miles from the sea. Similar conditions are met with on Vanua Levu, but there the belt is about 45 miles long.

Although sugar cane is the main crop in the two coastal belts, a small area of land in the Nadi district is now planted with pineapples and an area in the Tavua district is used for cattle raising. In Vanua Levu a considerable part of the dry coast is planted with coconuts. The non-agricultural land in both belts is mainly rolling hills covered with reed and bracken fern. Guppy, in his 'Observations of a Naturalist in the Pacific' (II, p. 548; 1906), gives an excellent description of this 'talasinga country'; but the reeds to which he refers as *Eulalia* can now be assigned to *Miscanthus japonicus* Anderss., and his 'yaka plant' is *Pueraria Thunbergiana* Benth., not *Pachyrrhizus trilobus* DC. Guppy's 'talasinga country' is that of Vanua Levu; but his description would fit also the corresponding coast of Viti Levu, except that I have seldom seen in Viti Levu some of the plants recorded by Guppy as common in the 'talasinga country' of Vanua Levu, e.g., *Cycas circinalis*, *Commersonia echinata*, *Acacia Richii*, and the *Hibbertia* (*H. salicifolia* Turcz.).

The orchid *Spathoglottis pacifica* Reichb. f., deserves a place in any list of the common plants of the 'talasinga country' of both islands.

Differences in the floras, such as the absence from the dry belt of Viti Levu of plants common in the dry belt of Vanua Levu, may be due to climate, and a list of many species could be compiled which are in the latter but not in the former.

The annual rainfall of the dry belt is about 65 inches in Viti Levu and slightly more in Vanua Levu. The dry belt of Vanua Levu is about 100 miles further north than that of Viti Levu. Most of the rain falls from January to March, and continues in decreasing showers into April.

Nearly all the sugar cane in these belts is raised by Indians, descendants of men brought from India under the indenture system; and, as one would

expect, many of the weeds among their holdings appear to be of Indian origin.

The sugar-cane lands of the leeward coasts of Viti Levu have been under intensive cultivation for 40-60 years. There were sugar mills earlier, but of a primitive type, and the land required to feed them cannot have been extensive. The lands of Vanua Levu have been under intensive cultivation for about 50 years. And 50 years is the time during which large numbers of Indians have lived on these coasts.

Seemann, in his 'Flora Vitiensis' (1865-73), names many weeds which he observed in 1860. Since then weeds have claimed little attention, yet were coming in, until it was realized in recent years that many were injurious and the 'Injurious and Noxious weeds Acts' were passed to try to cope with them. Horne, in 1877, and Guppy, 1896-99, collected in Fiji, but have not recorded much information regarding the weeds. Miss L. S. Gibbs, in 1907, and Sir Everard im Thurn between 1904 and 1910 collected chiefly in Fiji, but their attention was directed chiefly to the indigenous flora. Thus the reader will appreciate the fact that little has been published concerning weeds since Seemann wrote. The writer's work commenced in 1917.

Miss Gibbs wrote of the encouragement weeds in the mountains obtained when land was abandoned to return to forest after the methods of shifting cultivation employed by the Fijians. The sugar-cane lands are not exactly in the same position. Dry areas are common in the Pacific on the leeward sides of islands such as would seem never to have carried forest: and in those of Fiji, if the Indian cane grower abandons his ground, which is seldom, it does not return to forest but becomes waste.

Twenty years ago I noticed at Lautoka, the appearance of a fine crop of plants of *Centaurea melitensis* Linn., out of straw packing thrown on to a rubbish heap; but establishment did not follow and the plant has not been seen again. This is an illustration of what must happen often—a failure to reproduce; but such occurrences are rarely reported, and few data are available of other plants which have arrived and died out after arrival.

It is not proposed to discuss the means whereby weeds arrive; but mention may be made of the frequency of arrival in a seedsman's packet and subsequent escape from a garden.

One-third of the plants dealt with in the following pages were in Fiji in 1860 (*teste* Seemann): one-sixth of the others arrived perhaps before 1900, and the rest have arrived since then. Nearly half of the species are here recorded for the first time as Fijian.

Other introduced plants not previously recorded have established themselves in Fiji, but not on the leeward coasts, and here are some records, partly from the writer's collecting and partly from collections made by Mrs. Tothill:—

*Senebiera didyma* Pers. Nadarivatu, Greenwood, May 1941.

*Meibomia scorpiuroides* (Sw.) O. Kze. Kuntze Suva, Mrs. Tothill, March 1927.

*Desmanthus virgatus* Willd. Vanna Mbalavu, Mrs. Tothill, July 1927.

*Sesbania tomentosa* Hook. & Arn., forma *arborea* Rock. Nayau, Mrs. Tothill, July 1927.

*Caesalpinia sepiaria* Roxb. Suva, Mrs. Tothill, June 1927.

- Cassia siamea* Lam. Suva, Mrs. Tothill.  
*Passiflora edulis* Sims. Nadarivatu, Greenwood, September 1931.  
*Eryngium foetidum* Linn. Suva, Greenwood, August 1929.  
*Apium Anni* (Jacq.) Urb. Suva, Greenwood, April 1925.  
*Crepis japonica* Benth. Suva, Greenwood, January 1931.  
*Lobelia zeylanica* Linn. Nadarivatu, Greenwood, September 1931.  
*Isotoma longiflora* Linn. Levuka, Greenwood, June 1923.  
*Blechnum Brownii* (Sw.) Juss. Suva, Greenwood, August 1929.  
*Verbena bonariensis* Linn. Suva, Greenwood, April 1928.  
*Anisomeles ovata* R. Br. Levuka, Greenwood, June 1923.

As to the weeds of the leeward coasts, the writer's observations extend upwards to about 2,000 feet, and the records given do not refer to their occurrence in other parts of the islands, where they possibly behave very differently.

Many of the species have been determined at the Royal Botanic Gardens, Kew. Numbers in brackets in the text refer to specimens which may be found in the Herbarium of the Gardens. Other specimens may be found in the Herbarium of the Botanic Garden, Brisbane. A collection maintained in Fiji was destroyed by a hurricane in 1931. The writer desires to tender his thanks to the Director of the Royal Botanic Gardens, Kew, for the help given in determining the plants and to the Colonial Sugar Refining Company of Sydney for help they gave in enabling the collection to be made.

#### CRUCIFERAE.

BRASSICA JUNCEA Cosson. Subspontaneous, apparently through the last 30 years, in cultivated and waste land on the leeward coasts of both islands (301).

CARDAMINE SARMENTOSA Forst. In running streams and sometimes in Colocasia plantations between 600 and 1,000 feet elevation, in Viti Levu.

#### CAPPARIDACEAE.

CRATAEVA RELIGIOSA Forst. f. Near the mouths of several creeks in the Lautoka district (413).

GYNANDROPSIS GYNANDRA Briquet. Common and sometimes in sheets in cultivated ground (196).

CLEOME VISCOSA Linn. Common on the leeward coasts of both islands but not an aggressive weed (197).

#### BIXACEAE.

BIXA ORELLANA Linn. This, the 'Annatto shrub', occurs in several patches near Labasa, Vanua Levu, and Lautoka, Viti Levu.

#### PORTULACACEAE.

PORTULACA OLERACEA Linn. In cultivated land, particularly where sandy, throughout both coasts.

#### POLYGALACEAE.

POLYGALA PANICULATA Linn. Now rather common at Labasa, Vanua Levu, and in the Nadi and Sigatoka districts, Viti Levu (461). It was first observed at Labasa in 1923, and in the Nadi district about 1927.

## MALVACEAE.

*MALVASTRUM TRICUSPIDATUM* A. Gray. Common on both islands (100), chiefly in dry places; as a weed it is less aggressive than the following.

*SIDA RHOMBIFOLIA* Linn. Common, and on waste sandy soil in pure stands; frequent in coconut plantations; an aggressive weed.

*SIDA CARPINIFOLIA* Linn. Common on road-sides and waste ground, less abundantly in cultivated soil; not, like the last, in pure stands (99).

*URENA LOBATA* Linn. Throughout the leeward coasts of both islands up to 1,000 feet, sometimes as a troublesome weed.

*HIBISCUS DIVERSIFOLIUS* Jacq. Along ditches and in damp places; sporadic on the leeward coasts of both islands.

*HIBISCUS ABELMOSCHUS* Linn. On dry hills behind the leeward coast of Vanua Levu.

## STERCULIACEAE.

*WALTHERIA AMERICANA* Linn. Common chiefly in dry open hill-sides, from the shore to about 600 feet, in both islands.

## TILIACEAE.

*TRIUMFETTA BARTRAMIA* Linn. Common and making large patches on waste ground.

*TRIUMFETTA PROCUMBENS* Forst. f. On the sandy soil near the shore in the Sigatoka district, Viti Levu, but not spreading into cultivation.

*CORCHORUS TRILOCULARIS* Linn. Since 1921 or 1922 common near the coast in the Lautoka and Nadi districts, and at times making dense stands on damp soil, until in May or June it dies.

## OXALIDACEAE.

*OXALIS CORNICULATA* Linn. A weed of lawns and gardens, seeding profusely and increasing also by runners, common to 1,000 feet; not spreading much in sugar-cane fields. The sticky brown seed is thrown with force out of the explosive capsule and may be observed adherent to vegetation as much as three to four feet above the soil.

*OXALIS MARTIANA* Zucc. Sometimes a weed in bush houses and other damp places in the Lautoka and Rarawai districts of Viti Levu.

## SIMARUBACEAE.

*SURIANA MARITIMA* Linn. On pure broken coral at the northern end of Kadavu Lailai, an islet off the Lautoka coast. Guppy did not find it in Fiji in 1898, nor the writer when he visited the spot in 1919; but the shrub had obtained a hold before 1937. Mrs. Tothill has obtained it from beyond the limits of the dry coasts.

## MELIACEAE.

*MELIA AZEDARACH* Linn. A tree planted at one time as a possible source of firewood and now fairly common in the Lautoka and Ba districts of Viti Levu (266).

## RHAMNACEAE.

*ZIZYPHUS JUJUBA* Lam. Semi-naturalized in several places near Labasa, Vanua Levu, probably from introductions of about forty years ago (471).



## SAPINDACEAE.

*CARDIOSPERMUM HALICACABUM* Linn. Common throughout in the form which has been named *C. microcarpum* H. B. & K. Guppy suggested that birds spread it, but evidence has not been found that this is so. A cyanogen in it protects it against stock.

## LEGUMINOSAE.

*AESCHYNOMENE INDICA* Linn. Common in drains and other wet places, from Nadi to Penang along the coast of Viti Levu (214).

*ALYSICARPUS VAGINALIS* DC. Common in grass land up to 2,500 feet in Viti Levu and Vanua Levu. There is a passing mention of it in Fiji, in Miss Gibbs's 'Contribution to the Phytogeography and Flora of the Arfak Mountains' (London, 1917, p. 212). Stock readily eat it.

*DESMODIUM TRIFLORUM* DC. In the grass-lands of the dry coast at Lautoka; it is common but restricted to damp places (12). Stock eat it with relish.

*DESMODIUM HETEROPHYLLUM* DC. Sometimes in cane land and more often in pasture up to 2,500 feet, both in Viti Levu and Vanua Levu (518), on land rather more humid than *D. triflorum* demands. Stock eat it.

*CROTALARIA QUINQUEFOLIA* Linn. Only in the Tavua district, Viti Levu.

*CROTALARIA SALTIANA* Andr. Common through the dry coasts of Viti Levu and Vanua Levu, sometimes making thickets on cane land under long fallow (89). It is reputed poisonous, and the writer has never seen it touched by stock in Fiji.

*CROTALARIA RETUSA* Linn. In sandy places in the Lautoka district, Viti Levu (27); and sometimes intruding into cane lands.

*LOUREA VESPERTILIONIS* Desv. On dry grassy banks in the Penang district, Viti Levu, since about 1923 (740).

*CAJANUS INDICUS* Spreng. Naturalized from cultivation, but chiefly near farmsteads, in Viti Levu and Vanua Levu (213).

*CLITOREA TERNATEA* Linn. Common through the leeward districts of Viti Levu and Vanua Levu up to 200 feet, on roadsides and in waste land but not in cultivation.

*DOLICHOS LABLAB* Linn. Fairly common in waste places along the leeward coast of Viti Levu up to 1,000 feet, as well as in gardens.

*PHASEOLUS AUREUS* Roxb. (*P. Mungo*, auctt., non Linn.). On roadsides and in waste places in the dry belts of Viti Levu and Vanua Levu and sometimes in cultivated land, where, however, the plough soon destroys it.

*PHASEOLUS CALCARATUS* Roxb. Sometimes maintaining itself in cane fields in Viti Levu and Vanua Levu, maturing very rapidly and seeding. It was introduced in 1920 as a green manure. The flowers are often eaten by the Indian Bulbul, a bird which eats other Leguminous flowers also.

*PHASEOLUS SEMIERECTUS* Linn. On the dry coasts of Viti Levu and Vanua Levu, and in fallow land sometimes established in pure stands, smothering rival weeds, its weak stems leaning over each other (163).

*PHASEOLUS ADENANTHUS* G. F. Mey. From its natural place on the landward edge of the mangrove it spreads sometimes into low-lying cane

land nearby, but never plentifully. It occurs throughout the dry belts of Viti Levu and Vanua Levu.

*VIGNA CATIANG* Walp. Cultivated extensively and running wild at times in the dry belt of Viti Levu and Vanua Levu.

*VIGNA MARINA* Merrill. On pure sand-hills within a mile of the sea shore, in both islands (173).

*ATYLOSIA SCARABAEOIDES* Benth. Has spread since about 1925 through the dry coastal belt of Viti Levu up to about 100 feet, and when it intrudes into cultivation its deep tap-root makes it hard to dislodge (731).

*CANAVALIA ROSEA* DC. On sandy soils of the dry coasts of Viti Levu and Vanua Levu.

*MUCUNA ATERRIMA* Holland. Common in waste places as a consequence of extensive cultivation for green manuring, and thoroughly naturalized in both islands.

*SESBANIA BISPINOSA* (Jacq.), Fawcett & Rendle. Common near the coast in moist places between Ba and Ellington (747).

*INDIGOFERA SUFFRUTICOSA* Mill. Common, chiefly on sandy soils, in both islands, sometimes making impenetrable thickets on waste land. In the Sigatoka district it grows 7 feet high.

*TEPHROSIA PURPUREA* Pers. Common on the coast of Viti Levu and up to 500 feet; and although spreading into cultivated fields never so plentifully as to deserve the term weed.

*BAUHINIA MONANDRA* Kurz. A small American tree, now pan-tropic and established in waste places and about old Fijian villages on the leeward side of Viti Levu, especially in the Sigatoka district (773).

*CAESALPINIA PULCHERRIMA* Sw. In waste places and near old Fijian villages along the leeward sides of Viti Levu and Vanua Levu. It occurs with reddish-brown flowers and with golden yellow flowers and with flowers that are intermediate. It does not grow as a weed (84).

*CASSIA OCCIDENTALIS* Linn. Common on the coasts of both islands, up to 100 feet; frequently in cultivated land, but easily destroyed by cultivation. The name 'Rattle-pod', belonging to *Crotalaria Saltiana*, is sometimes applied to it.

*CASSIA HIRSUTA* Linn. Common near sea-level along the coast of Viti Levu (229).

*CASSIA TORA* Linn. Common, often in pure stands in cultivated land, along the coasts of both islands, but easily removed by cultivation.

*ACACIA FARNESIANA* Willd. Common at low elevations on the leeward side of Viti Levu, particularly in the Tavua and Penang districts, where it covers extensive areas. It is called 'Ellington Curse', from the injury it does about Ellington in the Penang district. Guppy, on account of its abundance on the coasts of Hawaii, experimented with the floatability of the seeds, but although they float for some time, man probably brought it to the Pacific islands as a garden plant. Cattle are recorded as eating the pods in Hawaii; but this has not been observed in Fiji.

*SAManea SAMAN* Prain. This, the 'Rain Tree', from extensive plantings has become naturalized. Trees in Lautoka, now 15 years old, have trunks  $7\frac{1}{2}$  feet in circumference at 3 feet from the ground. Cattle eat fallen pods.

*PITHECELLOBIUM DULCE* Benth. Near the coast in the Tavua and  
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Penang districts of Viti Levu, probably a consequence of planting about the Penang Mill some 50 years ago. It reproduces freely by seed and by suckers and is a pest in the Tavua district.

*ALBIZZIA LEBBECK* (Linn.) Benth. Often planted in the dry belts of both islands and naturalized in the Sigatoka, Rarawai and Tavua districts of Viti Levu. It is reproduced by seed and by suckers, but scarcely to the extent of being a pest (791). Trees 15 years old have an average circumference of  $5\frac{1}{2}$  feet at 3 feet from the ground.

*MIMOSA PUDICA* Linn. It is valuable in pasture, a pest in gardens and lawns, and sometimes troublesome in cultivated fields. Cattle graze on its young shoots in the pastures, the damper parts of which it covers. Ploughing suppresses it.

### CRASSULACEAE.

*BRYOPHYLLUM PINNATUM* Kurz. Waste places, usually where shaded, in the Lautoka, Rarawai and Tavua districts of Viti Levu (782).

### MYRTACEAE.

*PSIDIUM GUAYAVA* Linn. Common up to 300 feet, covering acres of flat land and rolling hills near the coasts of both islands; bird-distributed, principally by the Indian House Mynah (*Acridotheres tristis*), the Field Mynah (*A. ginginianus*), and the Indian Bulbul (*Moloplastes bengalensis*).

### MELASTOMACEAE.

*CLIDEMIA HIRTA* Don. A West Indian plant which has been naturalized in Fiji for sixty years. In the dry belt of Viti Levu it is found near Lawaga in the Sigatoka district and at the back of Penang Mill. In Vanua Levu it occurs near Laga Laga and Nibu, Wainikoro district. It is known as 'Koester's Curse'. Birds spread it; and the Government of the islands has imported from Trinidad the insect *Liothrips urichi* Karny as a check, which by feeding on the leaves weakens and has in many places killed the plant. Miss Gibbs (Journ. Linn. Soc. Bot. xxxix, p. 147; 1909) referred to *Clidemia* erroneously as *Melastoma denticulatum*.

### LYTHRACEAE.

*CUPHEA BALSAMINA* Cham. & Schlecht. A weed which arrived in Fiji about 1925, possibly from Hawaii, and is now in the Sigatoka district (786). The writer has found it at Nadarivatu, whence it may have spread down hill to the coast.

### ONAGRACEAE.

*JUSSIAEA SUFFRUTICOSA* Linn. Common in damp places, often in standing water, as in drains and at times in rice fields, in the dry belt of both islands (156).

### PASSIFLORACEAE.

*PASSIFLORA MALIFORMIS* Linn. Present in both islands and very plentiful in the Sigatoka district (216). The fruits have a characteristic taste. In common with *P. foetida* and *P. edulis* it fruits freely; *P. quadrangularis* fruits rather grudgingly and *P. laurifolia* only if artificially pollinated.

*PASSIFLORA FOETIDA* Linn. A South American plant which arrived during the last ten years and is now a weed in the Lautoka and Sigatoka districts of Viti Levu.

### CUCURBITACEAE.

*MOMORDICA CHARANTIA* Linn. Common in waste places and sometimes in cultivated land, at low elevations along the dry coasts of Viti Levu.

### AIZOACEAE.

*SESUVIUM PORTULACASTRUM* Linn. Common on mud flats behind the mangrove in the Sigatoka district of Viti Levu (784).

### UMBELLIFERAE.

*HYDROCOTYLE ASIATICA* Linn. Common in both islands up to 1,000 feet, preferring damp places, but not restricted to them, and sometimes in cultivated land.

*CORIANDRUM SATIVUM* Linn. Rather common on sandy soil in the Sigatoka district (70).

*FOENICULUM VULGARE* Mill. In waste shaded places near the Labasa Mill (653), not extending into cultivated fields.

### RUBIACEAE.

*OLDENLANDIA GALIODES* (F. Muell.), Benth. & Hook. fil. An Australian plant, established from thirty years ago, at Lega Lega near Wagadra, in the Nadi district, occupying depressions in the surface which appear to hold water in the wet season.

*HEDYOTIS AURICULARIA* Linn. Sporadic, chiefly on low hills, up to 1,000 feet in the dry belt of Viti Levu.

*BORRERIA VERTICILLATA* (Linn.) Mey. Common everywhere in grass-land and in cultivation along the leeward coast of Viti Levu up to 300 feet (151).

### COMPOSITAE.

*VERNONIA CINEREA* Less. Common along the leeward coasts of both islands, up to 1,000 feet.

*ELEPHANTOPUS MOLLIS* H. B. & K. A Mexican plant, now widespread, which may have arrived in Fiji about 1921 and has taken hold of the land somewhat in the Sigatoka district of Viti Levu up to 300 feet. It appears likely to become a troublesome weed chiefly on flat lands by rivers; it grows on hilly land also. It is spread by the winds which blow about dead detached tops of seed-bearing plants. *E. spicatus* Juss. and *E. tomentosus* Linn. are weeds of Hawaii, and the latter is troublesome in Rarotonga (Fosberg, 'Immigrant Plants in the Hawaiian islands', I, p. 8; 1937).

*AGERATUM CONYZOIDES* Linn. Not an aggressive weed, but everywhere along the leeward coasts of both islands up to 1,000 feet.

*ERIGERON FLORIBUNDUS* (H. B. & K.), Schult.-Bip. In cultivated land and on hills along the leeward coasts of Viti Levu, up to 1,000 feet.

*XANTHIUM ITALICUM* Moretti. A troublesome weed in the Penang and Rarawai districts and less so in the Lautoka district, Viti Levu; near sea-level near rivers. Its burrs are distributed by flood water as



well as by animals. It is locally known as the 'Noogoora Burr'. Cheel collected it at Tarawai in 1918 and recorded it as *X. chinense* Linn. (Proc. Linn. Soc. N.S. Wales, LIV, p. xlv; 1929).

*COSMOS CAUDATUS* H. B. & K. Common everywhere, sometimes in pure stands on waste land in both islands up to 500 feet.

*COSMOS SULPHUREUS* Cav. The 'Klondyke' *Cosmos* is sometimes seen naturalized near settlements in Viti Levu.

*TRIDAX PROCUMBENS* Linn. Common everywhere in both islands up to 2,500 feet.

*MIKANIA SCANDENS* Willd. This is locally called 'Mile-a-minute'. It occurs in waste and cultivated land, and climbs over trees lining creeks and the edges of clearings; throughout the leeward coasts of both islands. In the mountains it is a serious pest among Fijian food crops. It may be troublesome on cane land. The wind distributes its seeds.

*SYNEDRELLA NODIFLORA* Gaertn. Common everywhere on the leeward coasts of both islands up to 200 feet, but not aggressive (91). Perhaps it arrived about 1905.

*ELEUTHERANTHERA RUDEALIS* Schult.-Bip. An American plant first observed in the Penang district, Viti Levu, in 1930, and at Lautoka in 1939 (772).

*TITHONIA DIVERSIFOLIA* Hemsl. From cultivation in gardens, largely as a garden fence, it has spread to open waste places in both islands near sea-level (88). It stands trimming and easily strikes from cuttings. It would seem to have spread since 1905.

*EMILIA SONCHIFOLIA* DC. Common in both islands up to 2,500 feet, but not a troublesome weed.

*SONCHUS ASPER* Vill. Common in moist places in both islands from the coast to a considerable elevation.

*ERECHTHITES VALERIANIFOLIA* DC. A Brazilian plant which occurs on the hills behind the coast of Viti Levu between 800 and 2,000 feet. It may have arrived about 1895.

#### PLUMBAGINACEAE.

*PLUMBAGO ZEYLANICA* Linn. In waste places in the Lautoka district, Viti Levu, not abundant.

#### APOCYNACEAE.

*LOCHNERA ROSEA* Linn. In sandy soils in the Sigatoka, Nadi and Lautoka districts, Viti Levu, near sea-level (192).

#### ASCLEPIADACEAE.

*ASCLEPIAS CURASSAVICA* Linn. Common on the leeward coasts of both islands, in wet places and at times in flood water. It invades cultivation, but is not a troublesome weed. A native ally, *Tylophora Brackenridgei* A. Gray, has found the guava scrub of waste land in the Lautoka and Sigatoka districts a very favourable place and there smothers the guava bushes and associated plants.

#### GENTIANACEAE.

*LIMNANTHEMUM INDICUM* Thwaites. In still water in the Nadi and Sigatoka districts, Viti Levu, near the coast.

## CONVOLVULACEAE.

*CUSCUTA AUSTRALIS* R. Br. Common up to 1000 feet in both islands on a variety of host-plants, notably *Stachytarpheta*, *Cassia tora* and *Synedrella nodiflora*.

*IPOMOEA PES-CAPRAE* Roth. At the sea-margin, and on mud-flats behind the mangrove; common in both islands, but not spreading on to cultivated land.

*IPOMOEA BONA-NOX* Linn. In both islands, chiefly climbing over trees by creeks from the coast to low elevations. It is a nuisance in young coconut plantations sometimes.

*IPOMOEA QUAMOCLIT* Linn. A troublesome weed in cane fields in both islands (150), first noticed in the Lautoka district in 1918; spreading from garden cultivation.

*IPOMOEA COCCINEA* Linn. A more troublesome weed in cane fields than the last because of its greater size. It occurs in both islands and was observed first in 1920 in the Lautoka district.

*IPOMOEA TUBERCULATA* Roem. & Schult. Common in both islands in waste places (419), up to 200 feet.

*IPOMOEA CAMPANULATA* Linn. Among tall trees on the edges of forest and in waste land in the Sigatoka district, Viti Levu (306).

*IPOMOEA PHYLLONEURA* Baker. In the Lautoka district, Viti Levu, usually in wet places and sometimes in cultivated land (422).

*IPOMOEA TURPETHUM* R. Br. Common in both islands, sometimes invading cultivated land.

*IPOMOEA QUINQUEFOLIA* Griseb. In waste and in cultivated land in the Lautoka and Labasa districts, Viti Levu (199). In cultivated land it does less damage than *I. Quamoclit* and *I. coccinea*.

## SOLANACEAE.

*SOLANUM TORVUM* Sw. Common in both islands and a troublesome weed on river flats, particularly in the Sigatoka and Ba districts, where in places it forms pure stands. It has been proclaimed a noxious weed under the wrong name of *S. inamoenum*, and the name corrected subsequently. It seeds profusely and birds disperse the seeds. It seems to sustain scarcely any attack by insects; and stock do not eat it. It may have arrived in Fiji about 1890.

*SOLANUM OLERACEUM* Dun. Common in both islands to 1,000 feet in waste places, where if they are dry it flowers when only a few inches high. In the mountains it spreads much in moist shade.

*SOLANUM SODOMAEUM* Linn. In waste places in the Tavua district, Viti Levu (793), since about 1920.

*SOLANUM TETRANDRUM* R. Br. (*S. inamoenum* Benth.). Common on low hills along the coasts of both islands, up to 1,000 feet, but not in cultivated land, nor the pest that *S. torvum* is.

*DATURA STRAMONIUM* Linn. In waste places along the coasts of both islands, but scarcely plentiful.

*DATURA FASTUOSA* Linn. In waste places in the Lautoka district, Viti Levu (354), but not in cultivated land. Although unrecorded as Fijian, it would seem to have been in the island for thirty years.

*CAPSICUM FRUTESCENS* Linn. On the leeward coasts of both islands in waste places up to 200 feet.

*PHYSALIS MINIMA* Linn. A common annual in both islands up to 2,000 feet, often in cultivated land and appearing in pure stands. Birds disperse the seeds. *P. peruviana* Linn. grows in the mountains from 2,500 feet upwards. Both are called 'Cape Gooseberry'.

#### PEDALIACEAE.

*SESAMUM ORIENTALE* Linn. (*S. indicum* Linn.). As a weed in moist cultivated land in the Lautoka district, Viti Levu (262).

#### SCROPHULARIACEAE.

*VANDELLIA CRUSTACEA* Benth. In damp places on the leeward coasts of both islands.

#### ACANTHACEAE.

*THUNBERGIA ALATA* Boj. In waste shady places and sometimes in cultivated land in the Nadi, Lautoka and Rarawai districts, Viti Levu, from sea-level to 200 feet, common (205).

*THUNBERGIA FRAGRANS* Roxb. Fairly common in moist places and sometimes in cultivation in the Lautoka district, Viti Levu (735). The flowers are scentless, as elsewhere.

*ASYSTASIA GANGETICA* (Linn.) T. Anders. Sometimes in waste places in the Lautoka district, Viti Levu, but uncommon (738 A).

*RUELLIA AMOENA* Nees. In shady places usually in limestone country, in the Sigatoka district, Viti Levu (10).

#### VERBENACEAE.

*STACHYTARPHETA JAMAICENSIS* Vahl. On the leeward coasts of both islands. On dry waste land it covers acres, leaving no room for competitors, but is not troublesome in cultivation.

*STACHYTARPHETA MUTABILIS* Vahl. A common and aggressive plant on waste land in parts of the Nadi district near sea-level (455).

*CLERODENDRON FALLAX* Lindl. A shrub usually in heavy shade, occurring between Sigatoka and Penang at low elevations (11). Honey-suckers visit the flowers. Wilder ('Flora of Rarotonga,' Bishop Mus. Bull. LXXXVI, p. 92 ; 1931) stated that it was a pest in Rarotonga : it is not such in Fiji.

*LANTANA ACULEATA* Linn. (*L. camara* Linn.). Here and there near the leeward coasts of both islands and in Viti Levu to ten miles inland and up to 600 feet. Seeds are dispersed by birds. Two insect enemies have been established in Fiji for the purpose of checking it, the seed-eating fly, *Agromyza lantanae* Frogg., and the flower-eating Lepidopteron *Thecla agra* Hew. *Lantana crocea* Jacq. is abundant in the wet parts of Fiji and causes the death of cattle which eat it (*C. R. Turbet in Fiji Agric. Journ.* iv, no. 1, p. 24 ; 1931).

#### LABIATAE.

*OCIMUM SANCTUM* Linn. Frequently seen in waste places at low elevations in the Lautoka district, Viti Levu (64).

*OCIMUM BASILICUM* Linn. In waste places at low altitudes in the Labasa district, Vanua Levu.

*PLECTRANTHUS FORSTERI* Benth. In clearings and on waste land in the mountains, usually not below 500 feet, Lautoka district where it ascends to 2,000 feet.

*LEUCAS CEPHALOTES* Spreng. Rather common in wet places and at times on cultivated land in the Labasa district (658).

*LEUCAS DECUMENTATA* R. Br. From sea-level upwards to 1,000 feet in the Lautoka district, Viti Levu, increasing in abundance upwards.

*COLEUS AMBOINICUS* Lour. In open stony waste places, near sea-level Lautoka district, Viti Levu (734).

#### NYCTAGINACEAE.

*BOERHAAVIA DIFFUSA* Linn. Forming mats of vegetation on sandy soils at low elevations in the Lautoka, Nadi and Sigatoka districts, but not a troublesome weed.

*MIRABILIS JALAPA* Linn. Near Indian settlements and in waste places, somewhat rarely, at low elevations in the Lautoka district.

#### AMARANTHACEAE.

*AMARANTHUS MELANCHOLICUS* Moq. Somewhat common in waste places and on cultivated land; drought-resistant from its long tap-root and a rather troublesome weed throughout the leeward coasts of Viti Levu.

*AMARANTHUS VIRIDIS* Linn. In both islands common in waste and cultivated land where, like the last, it is difficult to eradicate on account of its long tap-root.

*ACHYRANTHES ASPERA* Linn. A common weed on the leeward coasts of both islands, from sea-level to the mountains, increasing in abundance upwards. It rarely invades cultivated land.

*ALTERNANTHERA TRIANDRA* Lam. (*A. sessilis* R. Br.). Common in waste and cultivated land from sea-level to the mountains, in both islands. It seeds very profusely.

#### CHENOPODIACEAE.

*BASELLA RUBRA* Linn. (*B. alba* Linn.). Common in waste places but seldom on cultivated land; in the Lautoka and Nadi districts, Viti Levu (394).

#### PHYTOLACCACEAE.

*RIVINA*, doubtless *R. humilis* Linn. In heavy shade, near sea-level in the Sigatoka district, apparently a new-comer, in about 1930

#### LAURACEAE.

*CASSYTHA FILIFORMIS* Linn. In both islands common in waste places, where it climbs over small trees and spreads over bare soil.

#### EUPHORBIACEAE.

*EUPHORBIA PILULIFERA* Linn. Common everywhere in both islands from sea-level to the mountains. It finds a place sometimes in cane fields. Some call it 'the Asthma Plant'.



*EUPHORBIA HETEROPHYLLA* Linn. On the leeward coasts of both islands, sometimes covering sandy soils in the Lautoka, Nadi, Sigatoka and Macuata districts (144). It flowers at the height of a few inches. Though so abundant it is scarcely a troublesome weed.

*EUPHORBIA CHAMISSONIS* Boiss. On the sea-shore of the leeward coasts of Viti Levu.

*EUPHORBIA DRUMMONDII* Boiss. Common in both islands on hard bare ground and in grass-land (154). It is recorded as a plant which in New South Wales yields hydrocyanic acid, but the author has failed in several trials to find that this is so in Fiji : flowering and flowerless plants have been used.

*EUPHORBIA ATOTO* Forst. fil. A beach plant common in both islands.

*PHYLLANTHUS SIMPLEX* Retz. From the coast to the mountains in both islands, springing up in the wet season and flowering with the incidence of the dry.

*PHYLLANTHUS NIRURI* Linn. From sea-level to 400 feet in both islands (208), in waste places and sometimes on cultivated ground. It can grow in the driest ground, and flowers when 2-3 inches high.

*RICINUS COMMUNIS* Linn. This, the Castor Oil plant, is found in waste places in both islands and at times as a weed in cultivated ground.

*JATROPHA CURCAS* Linn. In both islands at low elevations. Indians use stakes of it to serve as fencing and these take root. It is sometimes mis-named ' the Castor Oil Plant '.

### CERATOPHYLLACEAE.

*CERATOPHYLLUM DEMERSUM* Linn. Common in freshwater creeks and rivers along the Viti Levu coast.

### HYDROCHARIDACEAE.

*HALOPHILA OVALIS* Hook. A fairly common plant at low water mark on the coasts in the Lautoka district of Viti Levu.

### PONTEDERIACEAE.

*EICHHORNIA CRASSIPES* Solms. In fresh and brackish water in the Rarawai, Nadi and Sigatoka districts, Viti Levu. It seems to have been introduced as a garden plant about 1905. Now it is a noxious weed. It is common in the lower reaches of the Ba river and its first appearance in the Sigatoka district was about ten years ago.

### COMMELINACEAE.

*COMMELINA NUDIFLORA* Linn. In both islands from 1,000 feet upwards, a weed in plantations and common in damp places.

### LEMNACEAE.

*LEMNA OLIGORRHIZA* Kurz. From the coast to the mountains in Viti Levu, often covering small shaded pools.

### POTAMOGETONACEAE.

*RUPPIA MARITIMA* Linn. Found in brackish pools near the coast in the Penang district of Viti Levu.

## CYPERACEAE.

*PYCREUS POLYSTACHYUS* Beauv. A common weed in wet places in both islands (29), sometimes covering acres of low-lying ground, commonest near brackish water, but occurring also inland near fresh water.

*CYPERUS ROTUNDUS* Linn. Very common on flat land near the coasts of both islands and a troublesome weed in cultivation, where it is almost impossible of eradication if allowed to get well established. It forms nearly pure stands on river banks. A bare fallow during the dry season is a partial check on it.

*CYPERUS DIFFORMIS* Linn. Common in ditches and other wet places, as rice fields, near sea-level in both islands (479).

*CYPERUS COMPRESSUS* Linn. Common near Lautoka in damp places in the wet season (168), springing up in December and withering in April or May.

*MARISCUS LAEVIGATUS* Hook. & Arn. In ditches and other wet places in both islands.

*MARISCUS CYPEROIDES* (Linn.) Urb. In wet places in both islands (176 and 176 A).

*ELEOCHARIS CYLINDROSTACHYA* Boeck. In standing water in swamps, often covering considerable areas in the Lautoka and Nadi districts (439).

*KYLLINGA BREVIFOLIA* Rottb. In both islands from the coast to the mountains (35); sometimes a troublesome weed in lawns.

*FIMBRISTYLIS MILACEA* Vahl. Common in damp places near sea-level in Vanua Levu (584). It does not extend into cultivation.

*FIMBRISTYLIS MONOSTACHYA* Hassk. In the Lautoka district of Viti Levu, near sea-level (189) in places drier than suit most sedges and sometimes troublesome in lawns.

*FIMBRISTYLIS COMPLANATA* Link. A common plant in wet places in the Lautoka district, Viti Levu (173).

*FIMBRISTYLIS ANNUA* (All.) Roem. & Schult., var. *DIPHYLLA* (Retz.) Kükenth. In both islands up to 400 feet, often on dry hillsides, where it forms rather large clumps. It does not invade cultivation.

## GRAMINEAE.

Most of the grasses are weeds in cultivated land, but as they have all been dealt with in the 'Kew Bulletin', 1927, No. 1, and 1930, No. 6, I only give the most important here.

*ISCHAEMUM RUGOSUM* Salisb. On the leeward coast of Vanua Levu, and in Viti Levu in the districts of Rarawai, Nadi and Lautoka, near sea-level. A very troublesome weed in rice-fields, where it grows with the rice, and in the seedling state is hard to distinguish from the young rice-plants. When established it is very hard to eradicate.

*ISCHAEMUM ARISTATUM* Linn. A troublesome weed in the Labasa district, Vanua Levu, growing in wet places. The weak stems fall over each other and may make a cover a foot or more thick. It is hard to eradicate.

*IMPERATA EXALTATA* Brongn. In both islands from sea-level to the mountains, often in coconut plantations, but not a troublesome weed as a rule in cultivation. It spreads rapidly and will oust other grasses.

*SORGHUM HALEPENSE* (Linn.) Pers. In the Rarawai and Lautoka districts, Viti Levu, at low elevations. This, 'the Johnson Grass', is the worst cane-field weed of the Rarawai district. Thence it has spread to the adjoining parts of the Lautoka district. The most constant vigilance is being exercised by the Colonial Sugar Refining Company to keep it in check in the Nadi and Sigatoka districts: every patch detected being forthwith dug out and the plants destroyed. As its roots go deep and it seeds profusely the place remains under observation as a precaution against recurrence. It was imported as a fodder grass in about 1895, not 1905 (Kew Bull. 1927, p. 27), and soon became a weed.

*CHRYSOPOGON ACICULATUS* (Retz.) Trin. In both islands from the coast into the mountains. It is very common on low-lying ground. Its pointed seeds, attaching themselves to clothing, work through to the skin. Sloping ground, by its drainage causes the grass to die down in dry weather, but it reappears when the wet season commences. Mr. G. R. Robertson, of Lautoka, has observed that *Dichanthium caricosum* A. Camus smothered it in parts of the Nadi district. Therefore an experiment was tried in which a heavy growth of the Chrysopogon was planted through with the Dichanthium. In this experiment the latter spread, controlling the Chrysopogon. But on ground that is relatively dry both grasses die down together, and at the onset of the rainy season the Chrysopogon gets away and will more than hold its own. The Dichanthium spreads by runners which do not lie close to the ground but over the stems of the Chrysopogon. In lawns Chrysopogon requires cutting twice a week in wet weather and is apt to leave bare patches in dry weather.

*BRACHIARIA MUTICA* (Forsk.) Stapf. In both islands, an excellent fodder but a troublesome weed in cultivation, and, moreover, it blocks drains. It forms a very dense cover and grows rapidly.

*PANICUM MAXIMUM* Jacq. At low elevation in both islands. It is an excellent fodder, but a pest when it spreads in cultivation. This it does by seed: and removal is necessary before its seed time comes round.

## PROCEEDINGS OF THE GENERAL MEETING

5 March 1942

Dr. J. RAMSBOTTOM, O.B.E., M.A., Vice-President,  
in the Chair.

The Proceedings of the General Meeting held on Thursday, 19 February 1942, having been circulated, were taken as read and confirmed, after the name, 'Dr. C. R. Metcalfe', had been altered to 'Dr. R. Melville', in the report of the discussion on Dr. C. B. Williams' paper.

The thanks of the Society were recorded for gifts made since the last meeting:—From Mr. H. Atkinson, Mr. H. E. Forrest, Mr. C. H. Hooper, Dr. E. A. Nobbs and Professor F. E. Weiss.

The following Fellows signed the Obligation in the Book of the Charter and Bye-Laws and were admitted,—Basil Derek Wragge Morley, Param Nath Bhaduri and John Chear.

A Certificate of recommendation of the following candidate for Fellowship was read,—for the second time, in favour of Elizabeth Alice Flint.

The following candidates were balloted for and elected Fellows,—Stella Ross-Craig (Mrs. J. R. Sealy), William Glynn Burton, B.Sc., Professor Charles Earle Raven, D.D., Lt.-Colonel William Percival Cosnahan Tenison, D.S.O., and Hitendra Kumar Baruah, M.Sc.

The following candidate was balloted for and elected an Associate,—Willie Horace Thomas Tams.

The Vice-President in the Chair reminded Fellows that they are invited to make recommendations for new Members of Council and Officers.

The following communication was read and discussed :—

MR. B. D. WRAGGE MORLEY. Observations on the nest odours of Ants. (Discussed by Dr. Malcolm Smith, Mr. K. N. Kaul, Mr. A. J. Wilmott, Dr. B. Barnes, Mr. I. H. Burkill and the Vice-President in the Chair; Mr. Morley replied.). [Printed below, p. 109.].

The Vice-President in the Chair introduced the showing of three biological films by the GAUMONT BRITISH INSTRUCTIONAL, LTD :—

1. The Fern.
2. The development of the chick.
3. Maize.

(Discussed by Mr. H. Bruce Woolfe, Miss R. F. Shove, Mr. D. M. Reid, Miss Mary Field, Mr. John Chear, Mr. A. J. Wilmott, Lt.-Col. W. P. C. Tenison and the Vice-President in the Chair, who expressed the thanks of the Society to the Gaumont British Instructional, Ltd., for the showing of these films.)

The Vice-President invited Mr. Bruce Woolfe to speak.

MR. BRUCE WOOLFE remarked that although he approached the showing of natural history films to the Linnean Society with a good deal of trepidation, he was fortified with the thought that all the films produced by his Company were sponsored by well-known scientists, such as Dr. Julian Huxley, Professor Salisbury, etc. He thought it would be of interest to explain how these films came to be made. More than thirty years ago, Mr. Percy Smith gave up a position at the Board of Education in order to give his full time to what had up to then only been a hobby. Mr. Bruce Woolfe himself started to make natural history films in 1919; seven years later he was joined by Miss Mary Field. A good many years of hard going had thus been expended on pioneer work. The difficulties of the early days had been enhanced by the fact that there was no market for instructional subjects, and it was only possible to carry on the work by making two versions of the films, one for popular showing in the theatres, and an instructional version for use in schools. Enthusiastic scholastic authorities had gradually installed projectors, but it had been a very slow process, and it was only the success of the films in the theatres that had enabled the work to be kept alive.



In 1933 Gaumont-British decided that the time had arrived when instructional films should be made without the cramping effect of always considering theatrical requirements, and it was this gesture which had enabled the Company to secure the advice and help of leading biologists, with the result that a series of purely educational films had been produced during the last few years, of which some examples are shown this afternoon.

It had taken a very long time and a world war to convince the authorities in Whitehall that there was a use for the instructional film. Since the present war commenced all the Service Departments and several of the other Ministries had adopted the film for instructional purposes, and large numbers of projectors were now being brought into use. It was therefore felt that after the war it was quite likely that the market would be considerably extended and a possibility of making instructional films that would earn sufficient to pay for their production would at last materialize.

When the present war broke out the Company had to give up making this type of film owing to the general situation, but the British Council, realizing that British films of an instructional nature could compare favourably with any produced in other countries, have arranged to keep a certain number of films in production so that the continuity may not fail during the war. This will, undoubtedly, help the post-war situation.

The Company felt very gratified that the work they had done in the past could now be turned to good use in the war effort. They also felt that their time therefore had not been wasted, and hoped by seeing the films this afternoon the Linnean Society might be inclined to agree with them.

Miss R. F. SHOVE said the value of biological films depends largely upon their suitability to their purpose.

The two first films (Fern and Chick Embryology) are both technical and detailed, and would be of value when shown, for various purposes, to upper classes in schools; they would not be appreciated by the typical theatre audience.

The third film (Maize) is very different in character; it is simple, straightforward, expressed in non-technical language, and would be suitable for young classes studying natural history.

All three films are to be strongly commended for their excellent photography.

Mr. D. M. REID thanked the producers for such excellent records which he was sure would be of great importance in the teaching of Biology. They would save time and the cost of materials and give a balanced picture of complicated processes not easily achieved by mere description.

Mr. J. CHEAR suggested that it is very desirable that some standard of reference should be incorporated in plant films by which the scale of the speeding up would be made clear. This was done in the Chick film but not in the Fern film.

Mr. A. J. WILMOTT asked that, in films which were speeded up or slowed down, the actual differences in time scale should be stated in

terms of so many times normal rate, in order that the different appearances at the different speeds could be more easily compared. It was difficult, while watching the film, to work out the exact difference, in change of time scale, that a given number of hours or days in so many (estimated) minutes represented. He also asked that films should not be too quickly cut off when they showed a plant dying : the phenomena of the death itself, which might show features of interest, were often missing.

## OBSERVATIONS ON THE NEST ODOURS OF ANTS.

By B. D. WRAGGE MORLEY, F.L.S.

ANTS are for the most part blind, or nearly so, and they recognize friend or foe primarily by means of the olfactory sensillae situated in the antennae. Recognition is not, however, entirely by means of smell ; touch, sight (in the case of species where the eyes are better developed) and experience all playing an important but minor part. Now, while ants are able to distinguish the odour of their own or an enemy nest at a distance, they seem to be unable to recognize individual ants as friends or foes except at very close range, in many cases not until they are practically touching one another with their antennae. This distinction between friend or foe infers not only differentiation between ants of a different species, but also of a different colony ; for ants of the same species but a different colony may be equally regarded as foes. Hence the term 'Nest Odour' or 'Nest Aura', implying that each colony of ants has a distinctive odour. It is the function of the nest odour in the recognition of friend or foe that I am going to deal with in this paper.

Some myrmecologists appear to have assumed that actual antennal contact is necessary before recognition is effected. This is not the case ; careful observation during my experiments with mixed colonies of ants showed that recognition was effected in many cases while the ant was still at least its own length away from the enemy, the reaction being an immediate halt with antennae quivering and waving gently in the direction of the enemy, followed by an attempt at avoidance, immediate attack, or if recognition still seemed uncertain, a further rather tentative approach with mandibles extended ready for attack.

Miss Fielde, whose long series of experiments on the subject have been admirably summed up by Forel ('The Social World of the Ants,' London, II, pp. 27-58; 1928), demonstrated that it was possible to mix ants of different species, which were normally hostile, in observation nests, providing they were mixed when in the pupal stage, hatching out to form the mixed colony. A similar result was obtained when they were mixed up to twelve days after reaching the imago stage. These mixed colonies were not, however, of a permanent nature, fighting usually occurring after from four to six months. This would seem to indicate that the nest odour is not developed, or at any rate does not reach its full development, until some time after the ant has passed the callow stage and become fully adult ; but that there is some sort of inherited odour which is slow of development when the ants are isolated

when young from their fellow ants is shown by the final break-up of Miss Fielde's colonies.

The occurrence of species of ants which may be termed 'guest ants', which live in the nests of other species of ants; of myrmecophiles; of parasitic species of ants, whose queens are accepted and often forcibly dragged into the nests of the host species; and of slave ants which will fight ferociously against their own kith and kin—against the inmates of the very nest from which they were captured as pupae—all help to complicate the problem.

A further complication is provided by Miss Fielde's demonstration that if successive generations of ants born from eggs laid by the same queen be separated when in the pupal stage, a difference in the time of birth of two or three months will be sufficient to cause fighting when the ants are brought together again, although peace may eventually be established. She postulated a theory of progressive change in the nest odour to account for this.

In an endeavour to find some final solution of the problem I started, early in 1938, to experiment with artificially produced mixed colonies of ants, using, however, ants which were already fully adult.

Bethe had obtained temporary mixed colonies of adult ants by washing ants of various species in the blood of one species, and Miss Fielde had successfully mixed adult ants which had their antennae amputated; but obviously successful mixing would be expected when the ants had had their olfactory organs removed (Forel obtained a similar result by coating the antennae with paraffin, although he was not so uniformly successful). On 1 May 1940, however, I exhibited at a meeting of the Royal Entomological Society of London (Proc. Roy. Entom. Soc. Lond. (C), v, pp. 18, 23; 1940), an artificially produced multiple mixed colony of nine species of ants; mixing having taken place when the ants were already fully adult:—

- (1) *Acanthomyops (Dendrolasius) fuliginosus* (Latr.),
- (2) *Acanthomyops (Chthonolasius) mixtus* (Nyl.).
- (3) *Acanthomyops (Donisthorpea) niger* (L.).
- (4) *Acanthomyops (Chthonolasius) flavus* (Fab.).
- (5) *Formica rufa* (L.).
- (6) *Formica fusca* (L.).
- (7) *Myrmica ruginodis* (Nyl.).
- (8) *Myrmica laevinodis* (Nyl.).
- (9) *Leptothorax acervorum* (Fab.).

I have already published a short account of the technique used in obtaining these multiple mixed colonies (Morley, Proc. Roy. Entom. Soc. Lond. (A) xv, pp. 103-4; 1940), but in that paper I made no attempt to interpret my results. Today, in the light of other as yet unrecorded observations, further experience in the technique of producing these artificial colonies, and bearing in mind the results of past workers on the subject, I shall attempt such an interpretation.

The principle on which I worked to achieve the original mixed colony was to take species of ants which would not be entirely strange one to another, being likely to have met each other in their excursions outside

their various nests, and after accustoming them to life in a plaster observation nest, to mix them in conjunction with a base of species which had a strong odour and which they would not attack, and which would not attack them. The basic species in all cases was *Acanthomyops* (*Dendrolasius*) *fuliginosus* (Latr.).

In thus attempting to form these mixed colonies I made three assumptions:—(1) That the nest odour is at the most only a variation of the species odour, disregarding acquaintance with the nest odour, but considered acquaintance with the species odour as being a possibly important factor. The ants in most cases were taken from light colonies not close together. (2) That ants are capable of remembering odours with which they have been acquainted. (3) That the *fuliginosus* odour would to a large extent mask the various species odours concerned and that recognition of the species odour of any particular ant, masked in this way, would not cause fighting, because of factors (1) and (2).

The success of the experiments would seem to indicate that these assumptions were well founded, although points (1) and (2) needed further confirmation. That the nest odour is merely some slight variation of the species odour is also indicated by the fact that peaceable amalgamation of two colonies of ants of the same species may occur in the absence of any third species such as *fuliginosus*. I have observed such an amalgamation between two different colonies of *Myrmica scabrinodis* (Morley, B. D. W., Entom. Rec. 1, pp. 69-70; 1938). Since then I have achieved the same result with other species of *Myrmica*, *A. niger*, *A. mixtus*, *A. flavus*, and in some cases with *F. fusca*. These amalgamations may sometimes be disturbed by factors which give rise to intense activity or excitement, such as the introduction of another species of ant, or exposure to intense sunlight. Such break-ups seem to be especially easily caused in the case of *Myrmica*.

The reception of queens of parasitic species into the nests of the host species may possibly be explained in this manner, since the parasites are nearly always closely related to the hosts. The fact that it is possible to mix the guest ant *L. acervorum* with other species of ants in the absence of a third species might be explained by its having a very weak species odour, although its docile behaviour undoubtedly is a great aid to such mixing. I even succeeded in mixing this species with the very pugnacious *Tetramorium caespitum* (Linn.). A similar factor may be involved in the case of the parasitic species.

In interpreting these mixed colonies the factor of fear must be taken into account, it being often possible to mix two species of ants, although not very happily, when one of the species is present in very small numbers. It is possible that the presence of *Strongylognathus diveri* (Donis.) in the nests of *T. caespitum* is partly due to some sort of inherited fear.

The success of the multiple mixed colonies was undoubtedly chiefly, if not almost entirely, due to the presence of the *fuliginosus* with their exceptionally strong odour, which pervades the whole nest. And this weakens, to my mind, Forel's theory of topochemical smell ('The Social World of the Ants,' London, 1, p. 205; 1928). The whole trend of these experiments in mixing different species and colonies of ants points to the likelihood that the sense of smell in ants, while extremely highly



developed, need not be, and probably is not, so astonishing a thing as Forel and Brun would have us believe. It would seem that the idea that ants have to be able to distinguish between thousands of different nest odours is fallacious, and I fail to see the necessity for evolving such a complicated thing as a theory of 'cephorized smell' in order to explain olfactory memory. A discussion of Brun's experiments (Brun, R., 'Das Leben der Ameisen', Leipzig, pp. 186-199; 1924) would be out of place in this paper, since they were largely concerned with the development of the sense of smell in ants in connection with a different problem, but I do not think that they offer anything like the support for Forel's theory of topochemical smell that he and Forel claim.

In making some observations on a natural mixed colony of *A. fuliginosus* and *A. mixtus* (Morley, B. D. W., Entom. Rec. LI, p. 60; 1939) I found that the *mixtus* workers seemed to have got covered with the *fuliginosus* odour, even to the extent of seeming to be impregnated with it. Yet when the *fuliginosus* queen entered the original *mixtus* colony the odour must have been entirely *mixtus*. It would be interesting to know whether the *fuliginosus* odour is fully developed in the *fuliginosus* queen when she enters the *mixtus* nest.

To sum up: It would seem certain that as Donisthorpe ('British Ants, their Life-history and Classification', London, p. 48; 1927) and other myrmecologists have suggested, smell, memory, experience, education, touch and sight (in the case of those ants having more highly developed eyes, e.g. *F. rufa*), all have their part in the recognition of friend or foe, whether in the latter case of other species or other colonies. But the most important of these factors, and the basic recognition factor, is smell. I would suggest, however, that this question of species and nest odour has been made unduly complicated. It would seem to me most probable that there is a basic species odour, probably produced by a glandular secretion which may be expressed on to the cuticle, or is at any rate in some way exposed to the air, and that the individuality of the nest odour is imparted by slight deviations from the true species odour brought about by the ants licking one another, by their encounters with other ants and myrmecophiles, by their food and the materials from which the nest is made and other extrinsic factors.

That this species odour is slow of development is shown by Miss Fielde's mixed colonies, which lasted for several months. While another of Miss Fielde's experiments, when two species were soaked in distilled water for eighty hours, and those that survived mixed happily, would seem to indicate that the odour is produced by some substance which is expressed on to the cuticle. Bethe's washings also support this suggestion. That the nest odour is only a variation of the species odour is indicated by the fact that the amalgamation of two colonies of the same species can be brought about with remarkable frequency, although experiments of this nature have as yet only been tried on a few species. Greater difficulty is experienced when the species concerned are very pugnacious, but even then success can be obtained in some cases.

McCook ('Ant Communities', New York, pp. 221-2; 1909) managed to obtain a peaceful amalgamation of two colonies of *T. caespitum* already engaged in fierce combat in a jar, by placing in it a strip of paper

soaked in Eau de Cologne; although battle was rejoined after a few days, when the effect had worn off. The principle of the Cologne water is the same as that of the *fuliginosus* base; unfortunately, McCook carried his experiments no further.

The phenomenon of slave ants taking part in a battle against the inhabitants of the nest from which they were captured is difficult of explanation. Forel ('The Social World of the Ants', London, 11, pp. 10-11; 1928) records a case in which a *Formica sanguinea* (Latr.) nest was situated only ten paces away from a *F. pratensis* (Retz.) nest, from which it had captured cocoons which developed in the normal way into slaves. These *pratensis* then took part in a fierce battle brought about when he placed some workers from the *pratensis* nest on to the mixed nest, ferociously attacking their sisters. A possible explanation is that the licking and feeding of the *pratensis* by the *sanguinea*, together with their constant intermingling, had served to transfer to a large extent the *sanguinea* species odour to the *pratensis*, as in the case of the mixed *A. fuliginosus-A. mixtus* nest already mentioned.

Miss Fielde's progressive nest odour might equally be explained by the slowness in development of the nest odour indicated by her other experiments; the slowness in development of the nest odour causing a different intensity of odour or even none at all in some of the cases. Other extrinsic factors such as feeding, handling, the materials of the observation nests would also tend to produce differences, and it is improbable that sufficient control was exercised to nullify the possibility of such an alternative explanation.

The problem is not yet solved, but I think that the solution is to be found along the more simple and straightforward lines that I have indicated in endeavouring to interpret my results, rather than by the highly complicated theories put forward in the past. I would end by remarking that science has shown in the past that the most complex of problems are really of simple explanation, and that I think probably holds true in this case.

#### Discussion —

Mr. K. N. KAUL suggested that sandal-wood oil takes up scents well, and might be used, as with earth in India, to take up the scent.

Mr. WILMOTT said that it seemed difficult to imagine any chemical basis for odours of individual nests that could be related to species odour, as it would involve innumerable slight modifications of some chemical nucleus representing species odour. Nest odour, therefore, probably had an origin quite distinct from species odour.

Mr. WRAGGE MORLEY replied:—

A certain measure of success has been achieved in attempts to isolate the odour of *fuliginosus*, but in the case of other species where the odour is less easily perceptible, or even completely imperceptible, attempts have so far been unsuccessful. This Indian scent-preparation method would seem to hold considerable possibilities, and is certainly most interesting. The technique is so simple that practical difficulties in adapting the method for use in the case of ants would seem to be so limited as to be practically non-existent. I should imagine that better

results would be obtained, however, using some other medium than sandalwood oil.

The difficulty of obtaining such a great number of variations of the same chemical compound—and of one which would be likely to occur in a living animal—each having a slightly different odour which would be perceptible to the ants, although not to us, has always seemed to me to be a drawback to the theory of intrinsic nest odours. Apart from the chemical difficulties, which I am not in a position to judge, it would seem to be claiming for ants an olfactory sense of such remarkable development that one might almost term it a sense of ' stereochemical smell ', and I think that even more improbable than ' ephorized smell '.

Although ants of the same species do tend to use the same or similar materials in the composition of their nest, I think that there would be sufficient difference when considered in conjunction with the other possible extrinsic factors (myrmecophiles, feeding, etc.) to have the required effect. It should be remembered that ants differ greatly from most other insects in the flexibility of their behaviour in nest-building, and tend rather to use whatever materials are on the spot, than to go in search of special materials or conditions.

It is of interest in this connection that in the case of the wood ants (*F. rufa*, *F. exsecta* and *F. pratensis*) where the materials, habitat and habit in building tend to be more set, the whole populated area may be occupied by a single large polycalic colony consisting of, in some cases, over a thousand nests. In English woods this will practically always be found to be the case, but the number of nests is, of course, much smaller.

The action of ' Flit ' on ants is probably the same as that of sublimate, which is used to stop the ravages of the leaf-cutting ants of South America (the *Attini*) ; it gets on the antennae and temporarily deprives the ant of its olfactory powers, thus causing the ant to fail to recognize its friends. Since it is out of the nest and the deprivation is sudden the ant is more suspicious of the other ants which it meets and which it does not recognize, and a battle royal usually ensues. Deprivation of the olfactory organs does not always seem to have a pacifying effect similar to that of the masking of the odour, and such battles can be brought about in many species in observation nests when the antennae are treated in this way. Amputation, on the other hand, more usually brings pacification. The sudden pain caused by the sublimate probably has much to do with the occurrence of fighting in such cases, and it is also a factor which cannot be disregarded in amputation.

It would be expected that while close approach is necessary before recognition of individual ants can be effected, the cumulative effect of thousands of ants in the nest, the materials of the nest, guests, etc., would make recognition of the nest at a distance possible.

**PROCEEDINGS OF THE GENERAL MEETING**  
**19 March 1942**

Dr. E. S. RUSSELL, O.B.E., M.A., President,  
in the Chair.

The Proceedings of the General Meeting held on Thursday, 5 March 1942, having been circulated, were taken as read and confirmed.

The President called on the Botanical Secretary to pass to the meeting a communication from the Honorary Secretary of the Society for the Promotion of Nature Reserves. The Botanical Secretary therefore informed the meeting that the views expressed by the Conference on Nature Preservation in Post-War Reconstruction had been sympathetically listened to by the Minister of Works and Buildings, and that the Conference remains in being for consultation as and when required. Also that a list of areas which should be preserved for their natural history interest is being completed and that Fellows of the Linnean Society are asked to send, in confidence, through their delegates (in their case their Secretaries) items for such a list with the interest of each area stated. The Secretaries will gladly receive and pass on any suggestions which the Fellows are prepared to make.

The President announced that there were two vacancies in the list of Associates; and stated that some months would be allowed to elapse before the Council considered nominations.

In accordance with Chap. X. Sect. VIII. of the Bye-Laws, the following Fellows were elected, by show of hands, as Auditors of the Treasurer's accounts for 1941-42:—Representing the Council: Mr. R. H. Burne, Mr. D. M. Reid; Representing the Fellows: Dr. Isabella Gordon, Miss E. M. Wakefield.

The thanks of the Society were recorded for gifts made since the last meeting:—From Mr. E. St. John Burton and Dr. Nicholas Polunin.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted:—Lieut.-Col. William Percival Cosnahan Tenison, D.S.O.

A Certificate of recommendation of the following candidate for Fellowship was read,—for the first time, in favour of Ernest St. John Burton.

The President reported the death of Mr. J. L. Sager, Fellow of the Society.

The following communications were read and discussed:—

'Observations on the Smoke Fly (*Microsania*).’ By Dr. B. BARNES. (Discussed by Dr. B. P. Uvarov, Dr. Malcolm Smith and Dr. J. Ramsbottom; Dr. Barnes replied.)



*Abstract.*—

*Microsania* is a genus of the Diptera. The flies were regarded as great rarities until it was shown in Belgium in 1921 that they may occur in large numbers flying in the smoke from burning vegetable material. The flies were taken in small numbers in England in 1926 and 1930, and were seen abundantly in smoke in 1934. In 1938 and 1939, *Microsania pectinipennis* Meig. was common at and near Fernhurst, Sussex, either flying in groups in front of obstacles placed in the smoke from bonfires, or, in small numbers, flying singly in smoke or crawling on fresh ashes and the surrounding debris. No explanation is offered of this curious habit, but, as most of the flying insects seem to be males, and as females seem to keep close to the ground, it may be that the smoke gives an indication to the males of the presence of females, and so promotes mating.

The eggs, larvae, pupae and food of *Microsania* are not known. The life-history of the fly needs investigation. The association of *Microsania* with fires and the common presence on *Microsania* of mites belonging to the genus *Parasitus*, that is of mites known to frequent fungi, suggests a possibility that there may be some biological connection between *Microsania* and *Pyronema confluens*, an ascomycete which often appears very promptly in damp seasons on the sites of recent fires.

‘Distribution of the Whalebone Whales in the Southern Ocean.’

By Dr. N. A. MACKINTOSH. (Discussed by Dr. W. T. Calman, Dr. N. Polunin, the President and Dr. Malcolm Smith; Dr. Mackintosh replied.)

*Abstract.*—

Information on the distribution of whales is to be had from direct observation, from whale marking and from the catches of the whaling industry. In the southern summer Humpback Whales are to be found in about five well-defined groups around the Southern Ocean, and each group in winter migrates to the east or west tropical coasts of one of the continents to the north of it. The groups or stocks are thus segregated at both ends of their migration. In Blue Whales, and probably also in Fin Whales, there is a similar tendency, but a much less rigid segregation. Whale marking shows that in all three species individual whales, after the winter migration, usually return to the same region in the Antarctic.

This paper will be published in full in the ‘Discovery’ Reports.

*Discussion.*—

Dr. W. T. CALMAN said that Sir Sidney Harmer had had a good deal to do with devising the method of marking whales, and though some had thought that it would not have much result, it is evident that it has.

Dr. N. POLUNIN asked if the migration of whales had any connection with plankton.

Dr. MACKINTOSH replied that configuration of land was of importance, for some whales liked to be near coasts. So geographical conditions were of value, but it was doubtful if plankton had any horizontal effect.

'Contributions to the Flora and Phytogeography of SW. Greenland.'  
By Dr. N. POLUNIN. Discussed by Mr. A. J. Wilmott and Mr. J. H. Burkill; Dr. Polunin replied.) [This paper will be published in the Journal, Botany.]

*Abstract.*—

[This abstract indicates some phytogeographical problems concerning the area.]

Although it had long been considered by botanists to be one of the most thoroughly explored regions of Greenland, the Julianehaab sector in the extreme south-west can now be stated to have yielded in the summer of 1937 no less than twelve species (and a probable thirteenth) of vascular plants new to the entire 'continent'. These are as follows, the addition of 'confirmed' indicating that the species concerned had previously been claimed for Greenland but on erroneous or very doubtful grounds:—*Botrychium tenebrosum* A. A. Eaton; \**Potamogeton natans* Linn.; \**Hierochloa odorata* (Linn.) Beauv. (confirmed); *Agrostis gigantea* Roth; \**Agrostis tenuis* Sibth. (confirmed); *Poa flexuosa* Sm. (confirmed); *Danthonia spicata* (Linn.) Beauv.; \**Carex Mackenziei* Krecz.; \**Carex magellanica* Lam. (sensu lat.); \**Juncus balticus* Dethard. (confirmed); \**Gentiana Amarella* Linn. (cf. var. *uliginosa* Wahlenb.); *Antennaria compacta* Malte; *Montia rivularis* Gmel. ? (confirmed).

Of these twelve 'certainties' the seven starred belong to well-known major species that are circumboreal in range or at least widely distributed in more temperate regions on both sides of the Atlantic. All of these seven, except *Carex Mackenziei*, occur in Britain, where also *Agrostis gigantea* and *Poa flexuosa* are found. The remaining three 'certainties' are known outside Greenland only to the south or west, on or near the mainland of America. These observations are in conformity with the general relationships of the flora of south-western Greenland, which, as the geographical position would lead one to expect, seem on the whole more American than European (this is at variance with certain hypotheses of 'continental drift' in geologically recent times), and subarctic rather than truly arctic in type.

In addition to the above, many species and inter- or intra-specific entities were found in 1937 in the Julianehaab sector which had previously been thought to occur only farther north in Greenland, or in a few instances were apparently undescribed, with the total result that the known flora of the area visited was increased by some 10 per cent. in a single brief summer. So far it includes some 313 species of vascular plants, made up as follows: Pteridophyta 29, Gymnospermae 1, Monocotyledoneae 109, Dicotyledoneae 174. These figures include a few of the better established aliens.

This small area appears to be by far the richest floristically of all Greenland, whose known native vascular flora does not much exceed 400 species. An important factor contributing to this richness is the diversity of habitats which itself is largely dependent upon local climatic changes. Thus, near the exposed ocean coast the summer is cool and damp. Here, as on high mountains inland, the flora is limited and the vegetation depauperate, both being generally of arctic or alpine type, whereas away from the immediate coast the flora is less limited and the vegetation

more luxuriant, seal hunting giving way to sheep farming, though cod-fishing continues in the numerous fjords. Arctic plants persist in this zone chiefly on exposed hills and in depressions where the snow drifts deeply and melts too late each summer to allow closed vegetation to develop. Further in still, from some 40 kilometres inland and around the heads of the longer fjords and often up to the margin of the continental ice-sheet, the climate is noticeably more continental in type, with cold winters but relatively warm and sunny summers. It is chiefly here that the large but transient Nordic colonies were established some nine centuries ago, and it is in this 'Inner fjord zone' that *Salices* form a tall as well as dense scrub and *Betulae* in the most favourable situations reach the dimensions of small trees; here, too, that some crops are grown where there are any inhabitants and that most of the temperate plants persist, including almost all of the 'finds' listed above.

Among the plants found in 1937 in south-western Greenland were several, such as *Arenaria humifusa* Wahlenb. (*A. cylindrocarpa* Fernald), *Carex bicolor* All. and *Poa flarvosa* Sm., whose 'absence' from these or other parts of boreal America where they are now known to occur has been made much of by some phytogeographers in support of theories of 'persistence', etc. It now seems likely that it was the insignificant nature and restricted habitat of these plants that led to their being so extensively overlooked in the past, that they will in time be found in many more places where they were previously thought to be absent, and that in so far as their ranges may be 'disrupted' this may yet be explained without recourse to glacial history—e.g., by their calcicolous or other exacting requirements and extreme weakness in the face of competition which have combined in tending to restrict their possible habitats to the suitably 'open' ones which in general become fewer and fewer the farther we go south.

Recent opinions as to what number of species of phanerogams in the present Greenland flora were introduced by the Norsemen have varied from about 50 down to only 5. It now seems permissible to assume such ancient introduction in the cases of about 8 species and probably a smaller number of intraspecific entities among the phanerogams, including more than one from America.

## PROCEEDINGS OF THE GENERAL MEETING

16 April 1942

Dr. E. S. RUSSELL, O.B.E., M.A., President,  
in the Chair.

The Proceedings of the General Meeting held on Thursday, 19 March 1942, having been circulated, were taken as read and confirmed.

The thanks of the Society were recorded for gifts made since the last meeting:—From Dr. S. Maulik, Dr. N. Polunin, Dr. E. B. Worthington and the Carnegie Institution of Washington.

The following Fellows signed the Obligation in the Book of the Charter and Bye-Laws and were admitted,—Stella Ross-Craig and Prof. Charles Earle Raven.

The President reported the deaths of Capt. J. Guy Dollman and Mr. Charles Oldham, Fellows of the Society.

Recommendations for election to Fellowship were read,—for the second time, in favour of Ernest St. John Burton; for the first time, in favour of John Humphrey Bell.

The following communications were read :—

A discussion on 'The Biogeographic division of the Indo-Australian Archipelago, with criticism of the Wallace and Weber lines and of any other dividing lines, and with an attempt to obtain uniformity in the names used for the divisions.' Mr. J. B. SCRIVENOR, I.S.O., F.G.S. Geological and climatic factors affecting the distribution of Life in the Indo-Australian Archipelago. Mr. I. H. BURKILL, Bot. Sec. L.S. A history of the divisions which have been proposed. Dr. MALCOLM A. SMITH, Zool. Sec. L.S. The divisions as indicated by the Vertebrata. Dr. A. S. CORBET, F.R.E.S. Considerations based on the Rhopalocerous Fauna. [Printed in full, p. 120.]

## PROCEEDINGS OF THE GENERAL MEETING

30 April 1942

Dr. E. S. RUSSELL, O.B.E., M.A., President,  
in the Chair.

The Proceedings of the General Meeting held on Thursday, 16 April 1942, having been circulated, were taken as read and confirmed.

The thanks of the Society were recorded for gifts made since the last meeting :—From Mr. Frederick Chapman, the Carnegie Corporation of New York and the John Innes Horticultural Institution.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted,—William Glynn Burton.

The President reported the deaths of Dr. B. M. Griffiths, Mr. F. Flippance and Mr. J. W. Haigh Johnson, Fellows of the Society.

Recommendations for election to Fellowship were read,—for the second time, in favour of John Humphrey Bell; for the first time, in favour of Peter John Bell.

Mr. I. H. BURKILL exhibited a small tuber, 1 cm. in diameter, of the Black Bryony, *Tamus communis*, from a Devon lane, through which a runner of the Couch grass, *Agropyron repens*, had forced its way.



Dr. B. BARNES remarked that he had seen on several occasions the tubers of the potato traversed by stolons of this grass: and he called attention to recorded perforations of rubber balls (Journ. Roy. Hort. Soc. London, LXIV, Proc. xxix and cviii; 1938).\*

The Botanical Secretary read summaries of the communications of the last Meeting, towards a discussion on 'The Biogeographic division of the Indo-Australian Archipelago, with criticism of the Wallace and Weber lines and of any other dividing lines and with an attempt to obtain uniformity in the names used for the divisions.' In the resumption of this discussion the following communications were read:—Mr. H. K. AIRY SHAW, F.L.S., Some general considerations from the botanic standpoint; Dr. P. W. RICHARDS, F.L.S., On the Ecological segregation of the Indo-Malayan and Australian elements in the vegetation of Borneo; Dr. F. E. ZEUNER, On the divisions as indicated by the distribution of insects in relation to geology. [Printed in full below.]

A general discussion followed, in which Mr. J. R. Norman, Mr. J. B. Scrivenor, I.S.O., Dr. J. Ramsbottom, O.B.E., Dr. G. P. Bidder, Dr. F. E. Zeuner, Dr. B. P. Uvarov and Mr. K. N. Kaul took part.

The President suggested that the subject might be taken up again after the contributions already given had appeared in print.

The following paper was read:—

Dr. L. C. BEADLE. An ecological survey of some inland saline waters of Algeria. (Communicated by the ZOOLOGICAL SECRETARY.) (Discussed by Mr. A. C. Gardiner.) [This will be published in the Journal, Zoology.]

The President announced that the title of his Presidential Address would be 'Perceptual and sensory signs in Instinctive Behaviour'.

## **A DISCUSSION ON THE BIOGEOGRAPHIC DIVISION OF THE INDO-AUSTRALIAN ARCHIPELAGO, WITH CRITICISM OF THE WALLACE AND WEBER LINES AND OF ANY OTHER DIVIDING LINES AND WITH AN ATTEMPT TO OBTAIN UNIFORMITY IN THE NAMES USED FOR THE DIVISIONS.**

### **1.—GEOLOGICAL AND CLIMATIC FACTORS AFFECTING THE DISTRIBUTION OF LIFE IN THE ARCHIPELAGO.**

By J. B. SCRIVENOR, I.S.O., M.A., F.G.S.

THE object of this introductory paper is to indicate briefly such geological and climatic factors as may have influenced the present distribution of animal and vegetable life in the Indo-Australian Archipelago, known to many of us as 'Malaysia,' including the Malay Peninsula.

\* The following was received from Mr. C. E. Hubbard, F.L.S., a few days after the meeting:—'Last year, in breaking up a patch of rough grassland for an allotment, my spade cut through a large "sorbo" ball which had become partially buried in soil and humus. This ball had been penetrated in several directions by the rhizomes of Couch grass'.

In the area with which we are concerned the oldest rocks recognized so far with certainty are marine Devonian beds in Dutch New Guinea. The geological record from the Carboniferous Period onwards is much fuller, but only the latest stages of that record can be held to have had profound influence on the present distribution of life. Nevertheless, it is at least of interest to mention what the record tells us of the past. In Carboniferous times limestone was formed under marine conditions in Sumatra and the Peninsula, and in both there are remains of an Upper Carboniferous flora comparable with the European Stephanian flora. The position of this ancient Malaysian flora between the Gondwana floras of India and Australia is remarkable. There is also evidence of widespread vulcanicity that began in Carboniferous times and continued into Triassic times at least and spread over an area far greater than the present vulcanicity confined to the arc running through Sumatra, Java, the Lesser Sunda Islands, and then northwards to the Philippines. A rich marine fauna of Permian age preserved in sudden falls of volcanic ash has been found on Timor, Rotti and other adjacent islands, and is thought to prove an extension of the Tethys Sea to the eastward during the close of the Palaeozoic Epoch. During Triassic times terrigenous deposits were laid down in the Peninsula, Sumatra and Borneo, with cherts in some of which radiolaria are found, in others terrestrial plant remains. In the eastern portion of the Archipelago, particularly in the islands of the Banda Arcs, marine and terrigenous deposits of Triassic age indicate that by that time the present strong relief of islands separated by deep sea-troughs had already taken shape.

In Jurassic and Cretaceous times much the same conditions prevailed as during the Trias. On Rotti abyssmal deposits of Jurassic age are known and on Timor similar deposits of Upper Cretaceous age have been found consisting of radiolarian clay with sharks' teeth and manganese nodules, thus resembling modern radiolarian clay in oceanic depths. The proximity of this abyssmal deposit on Timor to the Java Deep on the one hand and the Weber Deep on the other is interesting, and will be mentioned again later.

With the beginning of the Tertiary Epoch we enter a period of much greater importance for our present purposes, dating back by about sixty million years. In the western part of the Archipelago the Lower Tertiary or Palaeogene rocks are terrigenous, while to the east limestone with *Nummulites* and *Alveolina* predominates, a clearly marine deposit. In Upper Tertiary or Neogene times the sea at first covered much of the present land surfaces, but towards their close a fall in sea-level, probably combined in the eastern part with earth-movements, produced that emergence of land which later still, during the Pleistocene glaciation of other lands, culminated in the union of Sumatra, Java and Borneo with the mainland of Asia to form Sundaland; while to the east the Sahul Shelf under the shallow sea now separating Australia from New Guinea was dry land also.

The geological factors likely to have affected the distribution of fauna and flora and that must now be considered, are as follows :—

- (1) Pleistocene depression of sea-level.
- (2) Rise of sea-level again at the end of the glaciation.

- (3) The two comparatively stable areas of the Sunda and Sahul shelves with an unstable area in between.
- (4) Distribution of rock-types that may have affected distribution of life.
- (5) Contours of the land.
- (6) Contours of the sea-bed.
- (7) Possible changes in position of land-areas.

1. Pleistocene depression of sea-level. It is now generally believed that at the height of the Pleistocene glaciation the amount of water accumulated in the ice-caps and the gravitational attraction of the latter resulted in a general fall in sea-level that went so far as to unite the larger western islands of the Archipelago with the Asiatic mainland. This old Sundaland provided an opportunity for Asiatic fauna and flora to spread southwards; while at the same time the union of Australia and New Guinea provided another opportunity for migration. Judging from the contours of the sea-bottoms on the shelves the fall in sea-level was about 100 metres (328 ft.).

2. Rise of sea-level again at the end of the glaciation. Melting of ice on the ice-caps restored the old sea-level at least, and we know from marine organisms in old beaches a few miles inland on the Sunda Shelf that the sea rose above its present level to about 50 feet. Whether it rose more than that is still uncertain. In the Peninsula sponge-spicules thought to be marine seemed to indicate a rise of 200 feet beyond the present level, but recently doubt has been expressed if these objects are sponge-spicules at all. Topography, however, in the Peninsula and in parts of Borneo, suggests to the author that the sea rose more than 50 feet, and that many isolated mountains now surrounded by land were once islands surrounded by sea.

3. The two comparatively stable areas and the unstable area between them. Earth-movements are now in progress in the area between the Sunda and Sahul Shelves, and they have been going on since at least late Tertiary times, probably much longer. Land-surfaces rising above the two shelves, however, are comparatively stable, by which is meant that they do not show evidence of great movement since late Tertiary times. That stresses in the crust had some effect on the massive rocks of Sundaland, such as the great granite intrusions, is shown by shearing of such rocks. We may feel fairly confident that in the comparatively stable areas the crust has not been modified by large vertical or horizontal movements, whereas we know that both have affected land surfaces in the unstable region. There are numerous instances of late Tertiary and Quaternary coral-reefs being raised to great heights, for example on Timor, where they are found at an altitude of 1,300 metres (4,264 ft.). These reefs are dated by Molengraaf as 'Plio-Pleistocene.'

4. Distribution of rock-types. There are two rock-types that must have had some influence on the distribution of life, though it may have been slight, namely, limestone and the volcanic rocks. Limestone, ranging in age from Carboniferous to modern coral-reefs, affects the distribution of flora that thrives on limestone and perhaps has a recognizable effect on the distribution of land-mollusca also. Limestone areas are greatly affected by solution in warm and wet regions, which results

in their having a very irregular surface difficult for large animals not adapted to mountainous habitats to traverse. Volcanic rocks, both ancient and modern, occupy a large area of Malaysia and can be divided into rocks decomposing into very fertile soils with a low percentage of silica, and those which yield poorer soils with more silica. We know that the violent eruption of Krakatoa in 1883 blotted out all life in that island-group, with the possible exception of an earthworm, and it is very probable that such catastrophes have happened before in the Archipelago, resulting in the gradual establishment of new fauna and flora.

5. Contours of the land. With the exception of the great alluvial plains, such as those of the east side of Sumatra, of West Borneo and the south coast of New Guinea, the contours of the land are abrupt, so that in making a traverse one may pass from low land to high land, and *vice versa*, quickly and in a short distance. The Malay Peninsula affords good instances of this. For example, Raub, situated nearly in the centre of the Peninsula, is only about 450 feet above sea-level, but has on either side and close by mountains rising to over 4,000 and 6,000 feet. There is, therefore, a probability of mountain floras and faunas being isolated and unable to spread owing to intervening low ground.

6. Contours of the sea-bed. On the Sunda and Sahul Shelves the contours are gentle and the depths nowhere much above 50 fathoms; but in the unstable area, to the south of Java and to the east of the Philippines, the contours are very steep and depths vary from shallow shore-line water to over 5,500 fathoms. On the shelves it would be expected that the uniformity of depths results in uniformity of fauna; but between them the sharp transitions from moderate depths to deep troughs, as in the Banda Sea, should result in considerable diversity of fauna.

7. Possible changes in position of land-areas. That the extent of the land-surfaces has varied greatly since late Tertiary times seems certain, and it is believed that some actual displacement of land horizontally takes place now in the unstable area, but nothing has been proved in the way of displacement sufficient to affect the fauna and flora. There is, however, one very interesting possibility that was pointed out by Wegener in his book on 'The Origin of Continents and Oceans' (English translation by J. G. A. Skerl, London, 1924). In his theory of 'continental drift' Wegener suggests that the islands of the arcs that include Java, Bali, Flores, etc., and those of the Bismarck Archipelago formed a continuous line in Neogene times, and that then the Australian block, including what is now the Sahul Shelf and New Guinea, drifted up from the south-east and broke through the line, distorting it in the process. It is an attractive suggestion that would help to explain why Timor, in the Outer Banda Arc, appears to have been pressed up against the Inner Banda Arc by a projection of the Sahul Shelf; why New Britain looks as though it had been dragged out of the line by New Guinea, and why Halmahera and Celebes possess such extraordinary shapes, as though they had been pushed bodily towards the north-west, leaving processes trailing behind. It might also help to explain the present isolation of the Weber Deep in the Banda Sea. It may once have been continuous with the Java Deep and the Philippine Deep, and the abyssal clay



now visible on Timor may have been formed in its continuation to the south-west. Later, the hypothetical arrival of Australia and New Guinea may have obliterated parts of this continuous deep trough and have raised by pressure some of its deep-sea clay to the surface on what is now Timor. If this movement of the Australian block did take place, carrying with it the Australian fauna and flora, the effects on the distribution of life in the Archipelago should be discernible.

*Climatic Factors.*—Passing now to climatic factors, a very important question is the nature of the climate in Malaysia during the Pleistocene glaciation. Dutch geologists say that in New Guinea the present snow-capped peaks are but a remnant of a former and much more extensive glaciation (H. A. Brouwer, 'Geology of the Netherlands East Indies', p. 39 : 1925). This alone is some evidence for a generally cooler climate over Malaysia in Pleistocene times. R. A. Daly, in propounding his theory of glacial control of coral reefs, said that the available information seemed to show that the whole of the Pacific was chilled during the Pleistocene glaciation and that corals, which cannot thrive in water below 68° F., were exterminated or greatly reduced as reef-builders. He said he found traces of a considerable glacier on Mauna Kea at about 3,600 metres (11,808 ft.). No glacial deposits, however, have been proved to exist at moderate altitudes, and palaeontological evidence of climate is not very satisfactory. The climate of the Philippines during Tertiary and Quaternary times has been discussed by Roy Dickerson (Gedenkboek van R. D. M. Verbeek; The Hague, 1925). He thinks there were no well-marked changes in the temperature of the Philippines and quotes Merrill in support of this conclusion. Both plants and mollusca are cited in evidence. He quotes Schuster, however, as thinking that in Pleistocene times a period prevailed in Java characterized by a more temperate and rainier climate than exists now. Merrill did not agree with Schuster and thought the Trinil flora very similar to that occurring at low altitudes today.

The chief point, however, is whether the climate in Pleistocene times had any effect on the distribution of the flora and fauna of today, and the answer must be left to other contributors to this discussion.

*Present-day Climate.*—8. Winds. Beginning in the south the area with which we are concerned includes a part of the Indian Ocean over which the steady SE. Trade-winds blow. F. Wood-Jones recorded in 1912 ('Corals and Atolls') that in the Cocos-Keeling Islands SE., ESE., or E. winds blow 300 days in every year. In the north are two monsoon areas, that of the Bay of Bengal and that of the China Sea. In a paper on 'The Journey of Fa Hsien from Ceylon to Canton' with monthly wind charts (Journ. Mal. Branch Roy. Asiatic Soc., Feb. 1941, xix, part 1), A. Grimes, Meteorological Officer, Straits Settlements, gives very full information about the winds throughout the year. In January and February the NE. monsoon blows about equally in both the Bay of Bengal and the China Sea, and at the equator the winds turn as from the NW. In March and April the China Sea is still swept by NE. winds, but variable winds blow in the Bay of Bengal and to the south of it. In May and June the SW. monsoon develops in both areas, but in June SE. winds blow on the east side of the Philippines. In August

and September the SW. monsoon blows in both areas, but changes towards the south over the Philippines. In October the NE. monsoon begins to blow over Formosa and the Philippines, and westerly winds set in over the Bay of Bengal. In November and December the NE. monsoon blows over both areas. Between the two monsoon areas and the SE. Trades variable winds blow over the islands of the Archipelago. Their extent alters considerably during the year according to the degree of penetration of the monsoons and the SE. Trades towards the equator.

9. Regions where seasonal variations are marked. Malaysia lies mostly within the equatorial belt, the limits of which can be taken as 5° N. and S. Latitude. On the north practically the whole of the Philippine group, a small part of British North Borneo and Kedah in British Malaya lie outside this belt. On the south the Sunda Strait, Java and the islands of the Banda Arcs as far east as the Kai Islands are beyond it. Both to the north and south there are fairly well-marked seasonal variations in the climate. In the Philippines there are three types of climate: (1) dry during the NE. monsoon and wet during the SW. monsoon, on the west side of Luzon, Mindoro, Negros and Palawan; (2) with no dry season and the maximum rainfall during the NE. monsoon, on the east side of the islands; and (3) an intermediate climate with no very pronounced rainy period and a short dry one of one to three months. The annual average of rainfall is 93 inches. Severe droughts occur and floods are caused by typhoons. At Baguio the absolute maximum rainfall observed during 24 hours in a typhoon was 879.8 mm. (34.6 ins.). In Kedah the rainfall drops from November to December, the moisture of the NE. monsoon being precipitated on the east coast of the Peninsula.

On the south of the equatorial belt the seasonal variations are more marked. Kupang in Timor shows a typical rainfall, high from December to March and low for the rest of the year, particularly in August and September, when the rainfall drops to considerably less than an inch per month.

10. Regions where seasonal variations are slight. These include practically the whole of the equatorial belt, characterized by heavy rainfall, great humidity and steady high temperature. Generally on Sumatra, Borneo and Celebes and on the Peninsula more rain falls during the NE. than during the SW. monsoon; but in the eastern islands, e.g. Ternate, off Halmahera, Ceram and Ambon, and also in places sheltered from monsoon winds such as Samarinda in Borneo and Gorontalo in Celebes, this difference is negligible, or, as in the cases of Ceram and Ambon, reversed.

11. Local variations of climate. These are caused by physical features modifying the effects of prevalent winds and sheltering land-areas from them. The climate varies in altitude considerably. For every 100 metres of height the temperature falls about 0.6° C. (1.08° F.). In the Peninsula local variations have been detected.

12. Temperature. In the Philippines the mean annual temperature is 26.9° C. (80.5° F.), May being the warmest and January the coolest months. Temperature sometimes rises as high as 42° C. (107.6° F.) and sinks to 12° C. (55.6° F.). For the Netherlands East Indies and the Peninsula the average annual temperature at sea-level is about 26° C.

(78.8° F.), the deviation being only a few tenths of a degree for the various stations, and the temperature is fairly uniform throughout the year. In July and August, however, it falls about 1.5° C. (2.7° F.) over an area bounded by lines drawn between Pontianak, Menado, Ambon and Kupang (Timor). In January and February there is a still smaller rise in the same area. The highest temperatures recorded are on the north coast of East Java and in Madura: the lowest at sea-level are found in the S.E., e.g. at Kupang, which has a mean temperature of 25° C. (79° F.) in July. The principal temperature changes are those between night and day which, in Batavia, average 7.3° C. (13.1° F.) for the whole year. In the Peninsula the temperature generally rises to 88° F. in the day and falls to 74° F. at night. Temperature in the sun is about 145° F. The highest temperature recorded up to 1929 in the Netherlands East Indies was 38.6° C. (101.5° F.) in Central Java: the lowest, on the plateau of Pengalengan, - 2° C. (28.4° F.), but lower temperatures must occur in the snow mountains of New Guinea.

13. *Precipitation.* This is entirely rain and dew excepting occasional hail-storms and snow or hoar-frost at very high altitudes. Space does not permit giving detailed information about rainfall, and the following must suffice as supplementing that already given. Kota Raja in North Sumatra has an annual fall of 65.66 inches with 124.2 days with rain. Lubok Sikaping in Central Sumatra has 169.83 inches with 240 days with rain. Kupang in Timor has 58.39 inches with 79.3 days with rain. Hill-stations have very high rainfall in some cases.

14. *Humidity.* This generally lies between 85 and 90 per cent., except where there is a pronounced dry-season. The highest mean monthly figure up to 1929 was 96 per cent. during September and December in Central Sumatra, and 95 per cent. during February in West Java. The highest yearly average of 93 per cent. was recorded on Mt. Singgalang. The lowest humidity recorded is 6 per cent. on Mt. Pangerango, West Java.

15. *Sunshine.* In the S.E. of the Archipelago there is less cloud than in Sumatra and Borneo, and in the dry weather the mean percentage of sunshine exceeds 90 per cent. Braak gives the following figures showing the effect of altitude on sunshine:—

| <i>Place.</i>      | <i>Height.</i>        | <i>Annual mean<br/>of sunshine.</i> |
|--------------------|-----------------------|-------------------------------------|
| Batavia.....       | 8 m. (26.2 ft.).      | 68 per cent.                        |
| Buitenzorg.....    | 240 m. (787.2 ft.).   | 63 "                                |
| Tjipetir.....      | 570 m. (1869.6 ft.).  | 52 "                                |
| Pasir Saronggo.... | 1200 m. (3936.0 ft.). | 49 "                                |
| Tjibodas.....      | 1400 m. (4592.0 ft.). | 43 "                                |
| Mt. Pangerango.... | 3020 m. (9905.6 ft.). | 41 "                                |

## THE BIOGEOGRAPHIC DIVISION OF THE INDO-AUSTRALIAN ARCHIPELAGO.

### 2.—A HISTORY OF THE DIVISIONS WHICH HAVE BEEN PROPOSED

By I. H. BURKILL.

DURING the last 150 years naturalists have grown increasingly interested in the systematization of the science of Biogeography. Just before the nineteenth century came in, Fabricius suggested a geography of insect-distribution. Then Alexander von Humboldt gained considerable praise for his *Essay on the geography of plants* (1805), and Latreille published, in 1815 and 1824, three sketches in distribution of different groups of animals.

Edward Forbes once suggested that the world might be divided into nine 'homozoic belts' and provoked a critic to comment 'life does not conform so simply to physical conditions'. Even earlier Swainson had written ('*Treatise on the Geography and Classification of Animals*', p. 7; 1835) 'circumstances connected with temperature, food, situation and foes are totally insufficient to account for the phenomena of animal geography'.

*Terminology: Region and Realm as terms of dimension.*—At the third meeting of the Linnean Society held in Burlington House (16 June 1857), not in this very room, but in one which the Society enjoyed earlier, Philip Lutley Sclater read a paper 'On the general geographical distribution of the class Aves'; and in that paper divided the world into six 'Regions' as follows:—

- (1) *Palaeartic Region*: Europe and the Mediterranean margin of Africa; northern and central Asia.
- (2) *Ethiopian Region*: The rest of Africa; Madagascar and probably part of Arabia.
- (3) *Indian Region*: India and eastwards to the Philippine Islands, Borneo and Java.
- (4) *Australasian Region*: Australia; New Guinea; New Zealand and Polynesia.
- (5) *Nearctic Region*: North America as far south as Mexico.
- (6) *Neotropical Region*: Central and South America; the West Indies.

Sclater did not particularize on boundaries, nor publish a map. For his purpose the Continents were not quite satisfactory; so he replaced them by *Regions*, continental in size.

In 1871 Blyth divided the world into seven Regions with 26 Subregions ('*Nature*', III, p. 427). In 1874 Sclater, who had turned his attention to mammals, divided the world afresh on new lines into Arctogaea, Dendrogeaea, Antaretogaea and Ornithogaea ('*The geographical distribution of Mammals*'). In 1876 Alfred Russel Wallace adopted Sclater's six Avifaunal Regions ('*Geographical distribution of Animals*'), and divided the Regions into 23 Subregions. Be it noted that Wallace's Regions, adopted from Sclater's first essay, are of continental size and that Wallace maintained all his life such size for studying distribution



to be appropriate (see 'Nature', XLIX, p. 610 : 1894). If Region be the term thus used, another term is needed for larger units of the earth's surface, and Realm, which has been employed by several writers, may be adopted, though there were American writers, e.g. Allen in 1876, Gill in 1885 and Heilprin in 1887, who substituted it for Region.

I must clarify the use of some more terms.

*A Protest against the use of 'Province'.*—In 1856 S. P. Woodward, in 'A Manual of the Mollusca', used Province, dividing the world into 27 Land-provinces and 18 Sea-provinces. He held, like many others of his time, that species had been created in 'specific centres' and by dispersal of individuals had come to occupy such areas as he could recognize, an idea he borrowed from Schouw, whose paper on 'The Origin of the Existing Vegetable Creation' had appeared in a translation from the Danish in Hooker's 'Journal of Botany' (II, p. 321, etc.) in 1850-51. Woodward's Provinces approximate in size to Subregions. But he was not to set a standard size. Indeed, in the year before, Sir Joseph Hooker and Thomas Thomson ('Flora Indica') had divided the land-surface of India into more 'Provinces' than Woodward the whole world, making no fewer than 64.

In 1892 a distinguished president of this Society, Charles Baron Clarke, in two papers, the one read to the Royal Society (Phil. Trans. vol. 183 B, p. 371) and the other in these rooms (Journ. Linn. Soc. Bot., xxxiv, p. 1), adopted the word 'area' in the place of 'region'. He divided his areas into sub-areas and these again into sub-subareas. He had been busy tabulating distributional data for 3,000 sedges and called his units 'tabulations areas'. His subareas numbered 23; and he wrote of them: 'I find by experience that 23 is quite the maximum number that can be worked by human infirmity on the first tabulation of 3,000 species'. Bowdler Sharpe adopted the word 'area' in the next year (Nat. Sci., III, p. 100).

To me the use of the word 'province' and, indeed, of any other word commonly employed in human administrative geography, is repugnant, for the simple reason that clarity is lost immediately a discussion is opened in which biogeographic provinces require to be defined by reference to administrative provinces. A like objection cannot be lodged against the adoption of 'Region' or 'Area'. But against 'Region' an objection can be lodged on other grounds, namely, because German botanists and followers of them use the word, actually in phytogeographic writings, for units of an entirely dissimilar value.

*The German word Gebiet.*—The Germans approach the problems of phytogeography through units called 'Gebieten' or territories. Grisebach in 1872 ('Die Vegetation der Erde') divided the world into 23 Gebieten, the number identical with Wallace's subregions, though the Gebieten themselves are not identical, and Grisebach had not accounted for Oceanic Islands within his Gebieten. Engler in 1882 ('Versuch einer Entwicklungsgeschichte der Pflanzenwelt', II) divided the world into 34 Gebieten with Provinzen as subdivisions of the Gebieten. Drude in 1887 ('Atlas der Pflanzenverbreitung') divided the world into 53 Gebieten as divisions of 14 Reiche. These German leaders in Plant-geography use the word *Region* for units of land (or sea) dominated by some particular feature in

the vegetation and, particularly, for belts on the mountains so dominated : and, unfortunately, the word has been used with this significance in books translated into English for students, as, for instance, Schimper's ' Plant Geography ' (Oxford, 1903).

*The term Region adopted.*—However, I am prepared to adhere to the use of ' Region ' in Selater's sense, with Subregion as its first division, so long as, following C. B. Clarke, the further subdivisions be termed Sub-subregions, Sub-sub-subregions in a logical manner.

I equate Gebiet with Subregion.

' Wallace's line '.—If P. L. Selater had published a map in 1857, I would reproduce the Indo-Australian part of it in this place : but he did not.

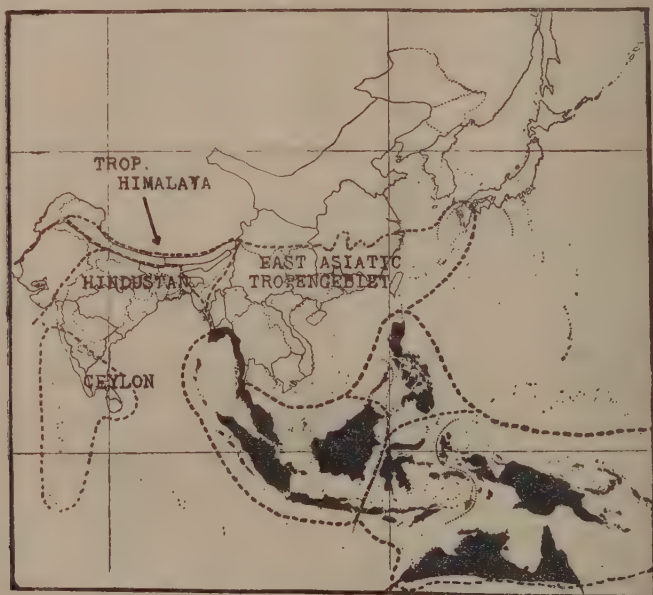


MAP No. 1.—Wallace's Oriental Region, with its subregions : (1) Indian, (2) Ceylonese, (3) Indo-Chinese, and (4) Indo-Malayan, being the Malay Peninsula and the islands as far as his alignment of the Wallace's Line. Also to the eastward his Austro-Malayan subregion, with his Polynesian Subregion to the north-east and his Australian Subregion to the south : these along with New Zealand comprised in his Australian Region.

He was content to say, on evidence got from the Birds (Journ. Linn. Soc., Zool., II, p. 130), that Borneo and Java go with India, and Celebes and Lombok with Australia. Günther in the next year (Proc. Zool. Soc. 1858, p. 373), on evidence from Reptiles, gave out that he approved of Selater's Regions. Wallace in 1864 (Proc. Zool. Soc. 1864, p. 276), discussing the distribution of parrots and, particularly anent the genus *Cacatua*, said that the narrow strait parting Celebes and Lombok from the islands to the west constitutes a biogeographical parting. Andrew Murray in 1866 (' The Geography of Mammals ') mapped it as such, save that he left the island of Bali on the east side. He placed the Philippines

on the west. Murray called all the Old World tropics to the west the Africano-Indian Region, and all to the east the Australian Region, using 'Region' as I would have 'Realm' used.

In 1868 Huxley published a paper on the classification of birds (*Proc. Zool. Soc.* 1868, p. 294) and discussed the north-westward dispersal of the Macropodidae as ending in the centre of the Malay Archipelago at the line Wallace had suggested between Borneo and Celebes; and to this line he gave the name 'Wallace's Line'. He laid it down as continued northward on the western side of the Philippines and then round them towards the East in the direction of Samoa. It is 'Wallace's Line' thus created by Huxley (see map No. 5) which is the focus of this discussion.

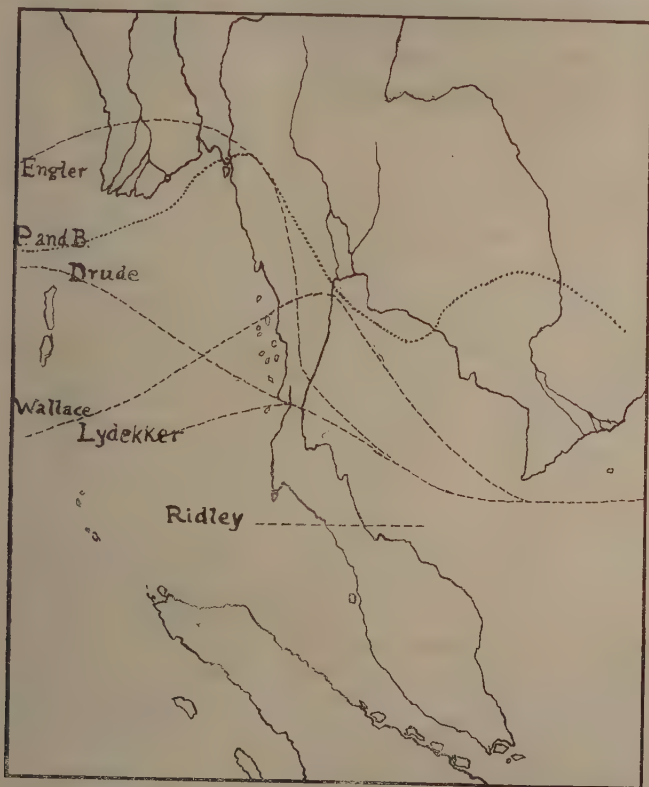


MAP No. 2.—Engler's Malayan Gebiet with three 'Provinzen'—Eastern province, Philippine province and South Malayan province, this last extending beyond the map to embrace Fiji. At the western edge of the map the Indian desert is assigned to a North African-Indian Steppe province which is part of an African-Arabian Steppe Gebiet.

In 1876 Wallace transferred the line to the east side of the Philippines where Murray had it, and he emphatically adhered to that alignment all his life.

In 1882 Engler (*op. cit.*) recognized a biogeographic line on either side of the Philippines, cutting off by the two a 'Provinz der Philippinen', or, as I would say, a Philippine sub-subregion. Towards 1924 a group of scientific men in Manila debated among themselves these lines and

concluded that the more pronounced of the two is the one Huxley laid down (see Dickerson in *Handel. derde Ned. Ind. Natuurwetensch. Congres*, reprint p. 2), and Merrill, reviewing the evidence, after exposing much in favour of Wallace's alignment (*Enum. Philipp. flowering plants*, 1, pp 77-154: 1926), concluded (p. 141) 'our present data seem to show that this fundamental line (Wallace's Line) does not turn to the east between Celebes and Mindanao but extends northward . . . and then eastward between Formosa and the Batan islands into the Pacific'.



MAP No. 3.—Biogeographic lines suggested by Engler, Prain and Burkill, Drude, Wallace, Lydekker and Ridley as parting Burma from British Malaya.

Of the southern end of the line Setchell in 1929 (*Rep. Proc. 4th Pacific Sci. Congress*, p. 311) suggested that there is a very sharp climatic break between Bali and Lombok.

*The Definition of a Subregion on the West Side of Wallace's Line; its various names.*—Having discussed Wallace's Line, we are ready to complete the demarcation of a subregion to the west side of it. The



southern part of the China Sea and the Indian Ocean obviously offer themselves for top and bottom, and we are left to determine the limit towards India. In this we immediately encounter disagreements. The best way of exposing them is by the map No. 3, whereon the several lines already proposed are marked. The disagreement is great, although it is agreed in the main that somewhere between Rangoon and Penang a line may be demarcated. The fact is that we have a bridge to consider, and the bridge is in itself of the nature of a belt. The line to be accepted across it completes the enclosure of our first subregion—a subregion of many names. It is Wallace's Indo-Malaya, Heilprin's Indo-malayan subregion, Engler's West province of the Malayan Gebiet, Drude's Sunda



MAP No. 4.—Lines suggested by various writers for delimiting the Oriental Region towards the north : (1) by the Sclaters, as the northern limit of their Indian Region ; (2) by Engler as the northern limit of his Palaeotropic Florenreich ; (3) by Lydekker as the northern limit of his Oriental Region ; (4) by Wallace as the northern limit of his Oriental Region ; and (5) by Drude as the northern limit of his Indian Floral Kingdom.

islands Gebiet, W. L. and P. L. Sclater's Malayan subregion, Molengraaf's Sundaland, and Merrill's Western Malaysia. I prefer the last name. Wallace's nomenclature was confusing ; he used Malaya for Western Malaysia when he excluded the Philippines and Indo-Malaya when he included them, an awkward antithesis. Van Steenis (*Gard. Bull. S.S.* ix, p. 88 ; 1937) advises that the term 'Malaya' be discarded in phytogeographic writings, and wisely so in view of the variable use that it has had.

*This Subregion as part of a Region.*—The Western Malaysian Subregion, by whatever name it be called, was made by Wallace one of four subregions which he gathered together into an Oriental Region, the others being his Indian Subregion, his Ceylonese Subregion, and his Indo-Chinese Subregion, as in map No. 1 above. This Oriental Region passed northward in Wallace's plan into his Palaearctic Region. In the following map (No. 4) his delimiting line is reproduced along with delimiting lines suggested by others as crossing the same part of Asia. I am unwilling to complicate our discussion by any detailed criticism of them, but would call attention to the dissimilarity between them, and would point out that both the lines, deepest in Thibet, were drawn by students of the Mammalia. It must be that this kind of animal by reason of possessing internal combustion for raising its body heat can overpass temperature lines which are stricter limits for cold-blooded animals and vegetation.

The region which we are discussing has been more misnamed than any other, e.g. Oriental by Wallace in disregard of many lands commonly known as the Orient, Indian by the Sclaters, while including within it much that is not India; and Malayan by Blanford in an effort to exclude parts of India with an African facies. I am unable to agree that the four subregions placed together by Wallace present to a botanist the semblance of a natural Region: two of the four, the Indian and the Indo-Chinese, have the year divided into halves by a summer peak of heat and a winter peak of cold, whereas the Indo-Malayan, because it is astride the Equator, has rain twice in the year at the times when the sun is over the Equator, and its year by this is divided into quarters; the remaining subregion, the Ceylonese, is intermediate, but a little more in agreement with the first two than with the third. Its position on the map suggests that it should be intermediate.

Engler, who did not recognize a major boundary at Wallace's Line, but assembled all the lands from the Atlantic to the remotest parts of the Pacific into one unit of Realm dimensions, called this unit the Palaetropical Floral Kingdom. Drude separated the African half and left the rest as an Indian Floral Kingdom.

*The Definition of a Subregion on the East of Wallace's Line.*—I return to Wallace's Line in order to discuss the Subregion to its immediate east—a Subregion much in debate. Here is map No. 5 showing various lines suggested as crossing it. I have given the history of Huxley's. Next comes Wallace's own alignment which, be it remembered, is not the line Huxley laid down when he bestowed the name. Wallace laid down his own line between Celebes and the Philippines and between Celebes and Borneo, but in his 'Island Life' (p. 432; 1880) he expressed doubts as to the propriety of the alignment, saying that Celebes might as well be regarded as on the one side of it as on the other. W. L. and P. L. Sclater, in 1899, sat on this fence and made a complete subregion of Celebes. It was a course to which Wallace could never have agreed, because he regarded his biogeographical classification as so intensely a matter for convenience that small areas—areas with the appearance of being oases—should not be raised to rank above what may be called their superficies value.

In 1894, that is five years before the date of the Sclaters' book, Weber, as the result of a study of freshwater fish, suggested that there is a line further east (Zool. Ergebn. einer Reise in Ned. Ost-Ind. III, p. 476). This line, slightly modified, received the name Weber's Line from Pelsencer (Bull. Acad. Roy. Belg. Cl. des Sci., 1904, p. 1001). Merrill (op. cit. p. 142) has suggested a further slight alignment to enclose Tenimber; and this is the alignment adopted on the maps in this contribution to our discussion. Lydekker would have the island of Halmahera placed to the west of it ('The Geography of Mammals', 1896). Other writers, taking Wallace's line as the western side of the subregion under discussion, have found the first reasonable boundary towards the east beyond the Solomon islands and New Hebrides. Engler found it beyond Fiji.



MAP No. 5.—Lines suggested by various biogeographers as crossing eastern Malaysia.

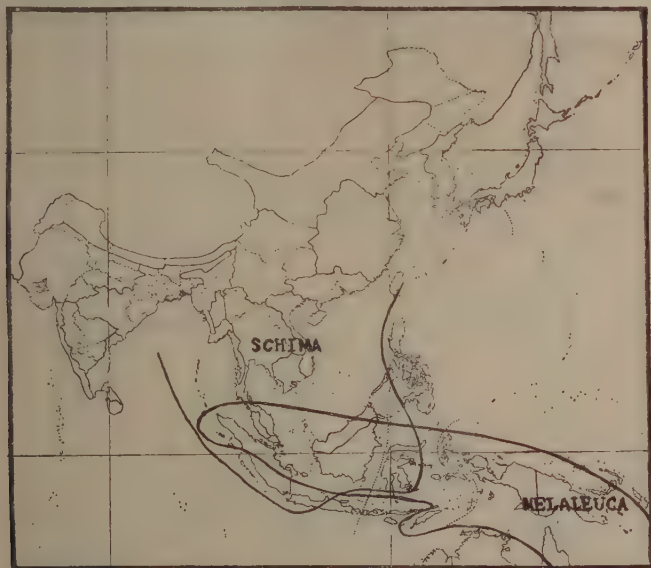
Admittedly there is a recognizable line beyond Fiji (see Hedley, 'A Zoogeographic scheme for the mid-Pacific' in Proc. Linn. Soc. N. S. Wales, 1899, p. 391, and elsewhere); but it is outside our immediate interest.

Why should there be so many possible lines in this subregion? Modernity of the land is the suggested answer: so modern that the complex of life has not yet settled down on it. To that I shall return, but before doing so would suggest that the possible lines have not been exhausted. Another line is suggested by the absence from the chain of the Lesser Sunda Islands of certain genera of plants, a line running more east and west than the other lines. To illustrate this I have borrowed from a paper by Dr. van Steenis (Bull. Jard. Bot. Buitenzorg,

ser. 3, XII, p. 250 ; 1932) two illustrations out of 16 which he gives of such distribution. I have selected these as opposites (map No. 6).

Dickerson (op. cit.) suggested that the unit of land (islands) between Wallace's Line and Weber's Line should be called Wallacea, a nice compliment ; but I prefer Eastern Malaysia or the Eastern Malaysian Subregion because this demands no explanation.

Merrill, in the 'Philippine Journal of Science' (XXIII, p. 1 : 1923), after dwelling on the stormy geological history of the Earth's surface between Wallace's Line and Weber's Line, on the powerful ridging due

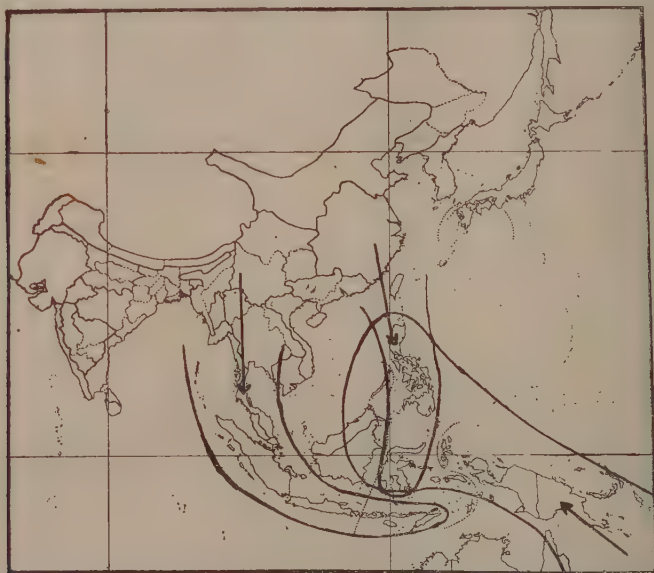


MAP No. 6.—The intrusive genera *Schima* and *Melaleuca* as they occur in the Indo-Australian islands, the one an invader from Asia, the other an invader from Australia : the first a forest tree of the lower hills, the second a tree of swampy lands.

to compression between Sundaland and the Sahul Shelf, and after demonstrating that the family of the Dipterocarpaceae which dominates the forests of Western Malaysia, requires long quiet periods of virgin forest growth to establish its hegemony, suggests that the poverty of Eastern Malaysia in these trees has been brought about by the way in which the crust of its Earth has been, time and time again, thrown into new barriers to infiltration. This poverty in Dipterocarpaceae runs on all fours with a poverty in Mammals stressed by Lydekker and others. No one doubts that there has been an infiltration into Eastern Malaysia from either side. As it is easier to follow the routes of mountain plants than of lowland plants because their routes are more circumscribed, I borrow another diagram from van Steenis (map No. 7).



Just as we found Peninsular Siam to constitute a belt, so does Eastern Malaysia constitute a belt. It is desirable to consider if it would not be well in matters of biogeography to admit that we cannot fit every bit of land to our complete convenience into such units as subregions and that we might have two kinds of units, subregions and belts. But the belt that is the Eastern Malaysian Subregion is of subregional dimensions. If we so recognize it, the definition of a Papuasian Subregion to the east of it becomes easy. This Papuasian Subregion comprises with New Guinea, New Hanover, New Britain, New Ireland, the Solomon Islands and the New Hebrides. But German botanists as Engler and Drude, add the northern coasts of Australia to Papuasias in an impractical



MAP No. 7.—The routes of mountain plants invading the Indo-Australian Archipelago, from van Steenis.

way. No tabulator could accept this, nor has it been shown justified by the plants and animals, see, for instance, Sir Spencer Baldwin's statement (Rep. Austr. Assoc. Adv. Sci. 15th meeting, 1921), 'for the most part the one striking feature of Northern Australia is the almost entire absence of anything like a luxuriant tropic vegetation or any abundance of animal life'.

At this point my indicating of boundaries must cease, lest we find ourselves with too many for the opportunity of approaching any decisions. The next map (No. 8) is a botanist's view of the Regions.

*A Botanical View of the Regions.*—We are interested in four, the Chinese Monsoon Region, the Indian Monsoon Region, the Eastern Equatorial Region and the Australian Region. They are founded on their vegetation, which again results from their climates, and to that I turn.

The greatest feature of the East is the enormously overpowering consequences of the great size of Asia which gets centrally hot in summer and draws in air bringing rain, and gets centrally very cold in winter and then pours out dry cold air over China and India, for from this results heat associated with moist conditions and cold with dry conditions. China being to the northward is more injured than India by the dry cold of winter, and still more so because it gets in a cataract winds which the Himalaya beneficially fends from India. The result is that there is sufficient climatic difference to establish a great difference in the Flora. It is true that in Southern China the finding of a defined line presents difficulties ; but to find an agreed line is certainly possible.



MAP No. 8.—Four phytogeographic Regions: (1) the Chinese Monsoon Region, (2) the Indian Monsoon Region, (3) the Eastern Equatorial Region, and (4) the Australian Region. The map with more detail in it, may be found in the *Annals of the Royal Botanic Garden, Calcutta*, xiv, pl. 81; 1936.

On the other hand, within the Tropics rain is to be expected when the sun crosses the Equator and the seasons are multiplied by two. Australia cannot repeat the phenomena of Asia because it is too small, but it develops characters of its own, and being in one of the belts of the Earth where physical conditions lead to drought, it is brought into sharp contrast with the nearby equatorial tropics. If we contrast this botanical view with the zoological view it is noticed that the botanist finds latitudinal lines more important than longitudinal, and the zoologist lays stress on longitudinal lines more than latitudinal when dealing with Regions. I want to stress this qualification 'when dealing with Regions'. It shows

the botanists and zoologists rather far from agreement, but I do not believe they are so far from agreement in the recognition of Subregions, and therefore we ought to talk to each other in terms of Subregions. If we can thereby reach a common nomenclature a considerable gain will follow. The officers of herbaria and museums where large stores of material must be so arranged that all is accessible to students, call for the world to be mapped out in the way best to them and they need well-determined and precisely fixed boundaries.

It is very interesting that the Mammalian and Avian views should be so un-botanical. Mammals and birds are late of evolution. Many forms of life had taken advantage of land bridges favourable early but broken down before mammals came to them; and it was on mammals and birds that so much of this geography was planned. If we seek to define Regions and Subregions on mammals and birds overmuch we evaluate the power of barriers of the last part alone of the earth's history. It has been claimed that it is right to do so. Then the Regions and Subregions are likely to lack interest among those who study older families.

## THE BIOGEOGRAPHIC DIVISION OF THE INDO-AUSTRALIAN ARCHIPELAGO.

### 3.—THE DIVISIONS AS INDICATED BY THE VERTEBRATA.

By Dr. MALCOLM A. SMITH.

IN an attempt to find a boundary line between the Oriental and Australian regions, I propose to start by defining the original limits of the two regions as they were in the past. This can be done by looking at a bathy-orographical map (such as the 'Times Atlas', map 61) and seeing the extent of the Sunda and Sahul shelves as defined by shallow water. At the end of the Pleistocene era, owing to glaciation and the consequent extraction of water from the ocean, these two shelves were dry land: the islands of Sumatra, Java and Borneo were a part of the mainland of Asia, and the island of New Guinea was joined to Australia. As far as the Asiatic region is concerned, no matter which group of vertebrates we study, we find that nearly every family, and indeed, nearly every genus now found on the great Sunda Islands, occurs also on the mainland of Asia, particularly Indo-China, and in a large number of cases the insular and continental species are identical. The fauna of the Great Sunda Islands is, in fact, much as we should expect it to be if they were part of the mainland. The similarity in faunas between Australia and New Guinea is not so marked, partly because Australia has had a much poorer fauna to offer New Guinea, but also because the climatic conditions of the two countries, at any rate at the present time, are very different to one another.

Between the two regions thus defined, lie a large number of islands, mostly small, and the problem is to discover how their faunas reached them.

There are three means by which this can have taken place: (1) by land connections, (2) by flight, for those creatures that have the power of

flight, and (3) by accidental transportation such as drift-wood or by boats through man's agency. I will take the last method first. It has, I believe, apart from flight, been a much greater factor in dispersal than is generally accepted. In connection with the Glacial Epochs we must remember also that the lowering of the ocean level which made the Sunda and Sahul shelves land, increased also the size of most of the islands that lay between them, so that the distance between any two was seldom more than 50 miles, and in most cases considerably less. To give one example, the distance between Borneo and Celebes at their nearest points today is about 90 miles; when the Sunda shelf was in existence it would have been only 25 miles. This proximity of one land



Map of the Sunda and Sahul shelves.

to another could play an important part in the dispersal of animals by drift-wood, and it is supported by a critical examination of the species which inhabit the islands. Disregarding subspecies, which are common in warm-blooded vertebrates, but comparatively rare in cold-blooded, one is struck by the fact, on going through the lists of species which have been recorded from the different islands, of the large numbers which are common to them all. And also that they are the species which are common and widely distributed on the mainlands from which they have come.

Due to climatic conditions, transportation by drift-wood is more common in tropical countries than it is in temperate. I can speak from personal experience in SW. Asia. It is a region of torrential rain-storms and periodical floods. Trees are uprooted by the floods, and



drifting away bearing other vegetation with them, become veritable islands, or natural rafts, of refuge for all sorts of creatures, particularly the small mammals, reptiles and amphibians that normally live on the ground. The larger mammals are able to flee before the advancing floods and seek refuge on higher ground elsewhere. According to Matthew, natural rafts, sometimes with living mammals upon them, have been reported several hundred miles off the mouths of tropical rivers, such as the Ganges, the Amazon and the Congo.

The possibility of drift-wood as a means of dispersal is further borne out by the story of the Island of Krakatau. This island, which lies midway between Java and Sumatra, and some 25 miles distant from them, was completely destroyed by volcanic eruption in 1883. Realizing the value of the island as a means of observing the repopulation of land, the Dutch naturalists have paid particular attention to it. It was visited by collectors two months after the eruption and again nine months after, and both parties have recorded that no sign of life was visible. On their last expedition which was made in 1928, that is 45 years after the disaster, they collected 47 species of vertebrates, 305 species of invertebrates, and a large number of invertebrates which have not yet been determined. The vertebrates include three species of bats, one rat with two subspecies, and which therefore presumably reached the island from two different sources, 36 species of birds, a crocodile, a python, and five species of lizards. The bats and the birds could have got there by flight, the crocodile certainly and the python possibly swam there, but the rats and lizards could only have got there by drift-wood or by human agency in boats. Of the total population the Dutch observers believed that about 90 per cent. could have been air-borne. Now, if all this can happen in 45 years, it does not require any imagination to picture what could have happened in the million odd years that have elapsed since the time when the Sunda and Sahul shelves were submerged by the rising waters.

The story of Krakatau, therefore, and an analysis of the species which populate the islands of the Archipelago, are, I think, overwhelming proof that a very considerable part of their faunas have reached the islands by air or sea, and did not require a land connection. Now for the species that cannot be explained in that way. The Philippines, Celebes and the Lesser Sunda Islands, as compared with Borneo, Java and Sumatra, are notable for the absence of large mammals, not because they could not have reached them, but because they could not survive upon them if they got there. Only small mammals occur in small land areas and generally the species are not numerous. None of the primates, the large carnivores, or the elephant, are to be found east of Wallace's Line. Two species of monkey (*Macaca maurus* and *Sinopithecus niger*), the Babi-rusa, a pig but without any known relative, and the Dwarf Buffalo (*Anoa*) are found on Celebes, and Palm Civets (*Paradoxurinae*) inhabit all the main islands as far east as the Moluccas. They came from Asia. From the Australian side species of Marsupial (Phalangery) occur on Amboyna, Ceram and Celebes. All these animals presumably reached the islands when they were connected to one another by land, but at what time and by what route we do not know. It is significant, however, that

except for the monkeys, all of them are primitive in type and have a long history behind them. The Sambar (*Cervus unicolor*), which is found on most of the islands, has, according to Wallace, been carried to them by man.

Except by a land bridge also it is difficult to explain the presence of amphibia, for with rare exceptions they are highly sensitive to salt water in any dilution, and are most unlikely to have made the sea passage. Excluding the Philippines, whose amphibian fauna is Asiatic in origin, some 36 species inhabit the islands lying between the Sunda and Sahul shelves. Some of them are indigenous.

As far as the freshwater fishes are concerned, Wallace's Line—his original one which passed to the east of the Philippine Islands—has been an emphatic barrier to their dispersal eastwards. Dr. Tate Regan, in an article written in 1909 but never published, states that all those fishes that have crossed it have either an auxiliary air-breathing apparatus, or are estuarine in habits, or are known to be carried by the natives as food. True, freshwater fishes, as he defines them, consist mainly of families which are confined to fresh water, and which we have every reason to believe have evolved their genera and species in fresh water; such fishes are of the highest importance as evidence of former land connections or of ancient lines of severance.

The only other vertebrate to be considered is man himself. He is not confined to limits as are the lower vertebrates, yet nothing is more striking when you leave Bali and pass on to the Lesser Sunda Islands than that the type of man has changed. The Malays have almost disappeared, and in their place are a people of Papuan type.

On the islands, therefore, between the Sunda and Sahul shelves there is a mixed population of animals of Asiatic and Austro-Papuan origin. The Asiatic species are most numerous on the Asiatic side, they get fewer in number as one travels east. The same condition is to be found if one starts from the Australian side. But over the whole area the Asiatic species are much more numerous than are the Australasian. That is to be expected, for Asia has had a much richer and more varied fauna to give than has Australasia. There is no evidence to show that climate has had any influence on the distribution of vertebrates in the islands.

It is not possible, therefore, to draw any line that will satisfy all groups of vertebrates and the best solution is to make a belt. Its western boundary would be Wallace's Line, modified as most vertebrate zoologists would like to see it, with Palawan to the west but not the rest of the Philippines, its eastern boundary Weber's Line. The Moluccan Islands, that lie to the east of it, although they were never part of the Sahul shelf, are so predominantly Papuan in their fauna that it would be wrong to include them. Of the two lines, Wallace's Line more clearly defines the limits of the Asiatic region than does Weber's Line the Australian. Yet if one had to draw a single line, it would be for the reasons just given, sounder to make it on Weber's Line rather than on Wallace's.

Weber's Line, originally defined by Pelseneer on the distribution of the vertebrates and the Mollusca, was also defined later by Boden Kloss. He based it primarily on geological facts and not on zoological, and

when he made it, he was not aware of Weber's Line. He drew it on what he called the volcanic fringe of Asia, in connection with which lie deep sea troughs, the deepest seas in the whole area. Whether volcanic action was responsible for the deep waters he does not profess to know. At two points, one between the Moluccas and Celebes, and the other between Timor and Australia, the line crosses shallower seas, and those he suggests were the bridges which connected the Australian and Indian areas. Other land bridges between Lesser Sunda Islands and Celebes, and Celebes and Philippines, have been proposed by the Sarasin brothers.

The region between Wallace's and Weber's Lines has been called 'Wallacea' by Dickerson, but he was not the first to define it. It also has the support of Merrill, who is a botanist and not a zoologist. He says (1926): 'In summarizing I would emphasize the conclusion that Wallace's Line cannot be abandoned in favour of Weber's Line or *vice versa*. Both are important, although neither is an absolute boundary between Asia and Australia when all groups of plants and animals are taken into consideration. No matter how convenient a simple line of demarcation would be, we must abandon the idea of a simple boundary and accept a region of transition as separating Australia and Asia, and this transition zone is the area between Wallace's and Weber's Lines'.

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THE BIOGEOGRAPHIC DIVISION OF THE  
INDO-AUSTRALIAN ARCHIPELAGO.4.—CONSIDERATIONS BASED ON THE  
RHOPALOCEROUS FAUNA.

By A. STEVEN CORBET, D.Sc., Ph.D.,  
British Museum (Natural History).

THE Rhopalocera are an important group as far as zoo-geographical boundaries are concerned, not only because their distribution is better known than that of any other division of invertebrate animals, but also because, with many species of butterflies, the colouring and pattern of the wings are modified considerably from one habitat to another, so that each island or island group has its own characteristic type of pattern.

Before making any extensive use of butterflies as indicator species in this connection, however, it is as well to consider one or two aspects of the matter which usually escape attention. In the first place, it must not be overlooked that much of the systematic work carried out by earlier investigators was based on the assumption of a constant wing pattern with any given species, a conclusion now known to be erroneous in many cases. As matters stand at present with many Rhopalocerus genera, specific separation must be regarded with some suspicion where structural characters have not been studied. In the second place, it is very evident that the advent of civilized man has resulted in much destruction of the forest with which the western part of the Archipelago was fairly uniformly covered two or three hundred years ago. One consequence of the appearance of large tracts of secondary plant growth has been a change in the butterfly fauna of the populated coastal districts, for cultivated areas which have been abandoned and are in various stages of reversion to forest are often remarkable for a profuse growth of flowering plants (mostly introduced from other tropical regions) which attract large numbers of comparatively few species of common and widely distributed butterflies: usually these ubiquitous species show little subspecific differentiation as regards colour and pattern from one country to another. A naturalist travelling from Europe to Canton *via* the Cape in the days of Linnaeus, and whose collecting activities were confined to a few ports, might well have concluded that the butterflies of Java and China were almost identical. When studying faunal divisions it is preferable to focus attention on the more local species, preferably those confined by primary forest, and perhaps montane or sub-montane in habit. The relative abundance and rarity should also be taken into account, but usually this is hardly possible, and most writers on faunistic divisions have to be content with the knowledge that an animal species is present or absent.

An obvious basis for work on the bio-geographical dividing lines in the Archipelago is to consider the presence or absence of certain genera or species of insects. As an illustration of the distribution of genera, the Lycaenid genera found in the Archipelago have been charted in fig. 1. The horizontal lines indicating the differing genera (names omitted) show the countries in which they occur, dotted lines being used for islands from which



the genera are as yet unknown, although probably awaiting discovery. The twenty-eight genera found throughout the Archipelago have been omitted. It will be seen that the Large Sunda Islands share a number of genera not found in the Philippines, and this favours the passage of the Wallace Line northwards between Palawan and the Philippines rather than between these islands and the Celebes.

A typical example of the results obtained by a consideration of the distribution of species is given by the Nymphalid genus *Tanaëcia* Btlr. This genus is more or less confined to Malaysia, and, with members of the *T. pelea* (F.) group, the wing colour and pattern is characteristic of the habitat rather than of the species. It is, in fact, often easier to fix the country of origin of a *Tanaëcia* specimen than to determine its specific identity (Corbet, in Ann. & Mag. Nat. Hist. ser. 11, VII, p. 507, pl. vi; 1941).

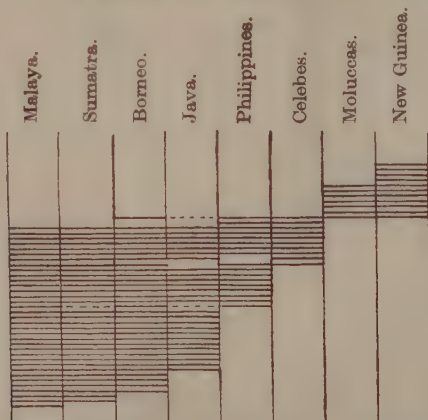


FIG. 1.—Distribution of Malay genera of Lycaenidae.

The Peninsular representatives of the *pelea* group are pale greyish ochreous brown with the hindwing border white; the Sumatran races are a rich chocolate purple-brown with the hindwing border washed with purple-blue; the Bornean races are usually paler with the blue bordering less extensive, and they differ also in that the white helmet-shaped spots in spaces 2 and 3 on the forewing are separated from the post-discal band. The few Javanese and south Burmese races are also distinctive. The Bornean subspecies of *T. munda* Fruh. show a curious form of polymorphism, occurring in a number of forms, some of which simulate the corresponding Malayan and Sumatran races.

In Table I are shown the countries in which the different *Tanaëcia* species occur. In fig. 2 a, the intensity of the dividing lines between adjacent Malay islands based on a consideration of these *Tanaëcia* forms is shown by the heights of the columns. These heights have been calculated from the formula

$$\text{height} = (T - c) / T,$$

where  $T$  is the total number of species found in any pair of adjacent

islands, and *c* is the number common to both. Adjacent islands with no species in common share a column extending from the base to the dotted line. When this method is applied to other genera of butterflies, rather similar results are obtained. Fig. 2*b* is based on the distribution of the thirty odd Malay species of *Euploea* F., a Danaid genus which is well known, as many of the species are believed to serve as models in mimetic associations.

TABLE I.  
Distribution of Species of *Tanaëcia* Btlr.

|                                 | Malaya. | Sumatra. | Borneo. | Java. | Bali. | Philip-<br>pines. |
|---------------------------------|---------|----------|---------|-------|-------|-------------------|
| <i>T. leucotaenia</i> . . . . . | —       | —        | —       | —     | —     | ×                 |
| <i>T. calliphorus</i> . . . . . | —       | —        | —       | —     | —     | ×                 |
| <i>T. pelea</i> . . . . .       | ×       | ×        | ×       | ×     | —     | ×                 |
| <i>T. palguna</i> . . . . .     | ×       | ×        | —       | ×     | ×     | —                 |
| <i>T. munia</i> . . . . .       | ×       | ×        | ×       | —     | —     | —                 |
| <i>T. clathrata</i> . . . . .   | ×       | ×        | ×       | —     | —     | —                 |
| <i>T. aruna</i> . . . . .       | ×       | ×        | ×       | —     | —     | —                 |
| <i>T. orphne</i> . . . . .      | —       | —        | ×       | —     | —     | —                 |
| <i>T. amisa</i> . . . . .       | —       | —        | ×       | —     | —     | —                 |
| <i>T. elone</i> . . . . .       | —       | ×        | —       | —     | —     | —                 |
| <i>T. coelebs</i> . . . . .     | ×       | ×        | —       | —     | —     | —                 |

Reference has been made already to the mutation in wing pattern and colour shown by some butterfly species on passing from one country to another, and often with a group of allied species a more or less similar pattern persists in an island or group of islands and then changes abruptly on passing to another island group. It is evident that these modifications in wing pattern may throw some light on the subject of faunistic divisions of the Malay Archipelago. The genus *Euploea* is quite remarkable for the similarity in wing pattern shown by different species found in the same habitat (Corbet, in Ann. & Mag. Nat. Hist. ser. 11, ix, p. 253 ; 1942). For instance, with many species in Burma, the forewing is a deep shining blue, almost unspotted, and the hindwing has a prominent series of white spots. In Neomalaya (Malaya, Sumatra and Borneo), the corresponding forms are similar to one another, and differ from the Burmese races in the much reduced or obsolete blue colour and in the obsolescent white spots on the hindwing: Javanese races are rather similar, although smaller, more drab in appearance and with a tendency for the forewing to be spotted. The blue colour of the forewing may return in Luzon, where there is always a large white subapical patch on the forewing. The races from the Celebes are larger and with prominent median and/or post-discal white spots. The forms from Timor are usually blacker than neighbouring races and with prominent white spots or bands on both wings. The races from the Moluccas and New Guinea resemble one another somewhat and are reminiscent of the Malaysian forms, a case not without parallel as far as butterflies are concerned and emphasizing the anomalous position of the Celebes, from the zoo-geographical standpoint, situated between the Moluccas and Borneo.

Grouping of the islands of the Archipelago according to the character of the wing pattern of the *Euploea* butterflies gives results similar to those obtained by the presence or absence method just described, but it must not be overlooked that this phenomenon of parallel variation may be attributable to some extent to local conditions and may be connected with certain climatic factors. Cases can be cited where *Euploea* species in widely separated islands have the same type of wing pattern (compare *E. algea* (Godt.) from Guam and Christmas Island).

The case of *Euploea tulliolus* (F.) in Australia is a good illustration of the complexities to be found in this subject of animal distribution. This widely spread species occurs from Indo-China, through the Archipelago, to the South Seas. As usual, the Timorese form is black and prominently spotted with white, while the Papuan race is dull brown with rather obscure violaceous spots on the forewing: there is every



FIG. 2.—Intensity of the zoo-geographical dividing lines between the Malay Islands based on the distribution of species of *Tanaëcia* Btlr. and *Euploea* F.

reason to believe that these comprise two geographical races of a single species. Now, in the Northern Territory of Australia there occurs a form of *E. tulliolus* closely allied to the race from Timor and, in fact, may have reached Australia from this island. This same form is found in Queensland, where it reaches Mackay in the south (Waterhouse, 'What butterfly is that?' p. 75; 1932). In Queensland, however, is a second butterfly so closely resembling the New Guinea representative of *E. tulliolus* that its Papuan origin can hardly be questioned, but in Queensland the two forms fly together and apparently do not interbreed and so must be regarded as separate species. As far as is known,

geographical races of *Rhopaloceros* species differ, almost invariably, by a large number of genetic factors, so that interbreeding between two allied races gives rise to a long series of intermediate forms (Waterhouse, in Proc. Linn. Soc. N.S. Wales for 1922, XLVII, p. ix : 1922 : for 1923, XLVIII, p. xiii : 1923). The complete absence of such intermediate forms of *E. tulliolus* in Queensland strongly supports the view that the two forms under consideration are here behaving as specific entities.

This overlapping of geographical races which appear to be functioning as distinct species is a phenomenon of some importance in the subject under discussion, for these overlaps occur on the peripheries of the distinct sub-regions.

There are a number of such overlaps in the Malay Peninsula, and there is little doubt that an explanation is to be found in the intermingling of geographical races which were formerly separated. For prolonged isolation of neighbouring races of a single species must result eventually in these races becoming too widely separated structurally for any interbreeding to be possible. Thus, if any subsequent reunion occurs, possibly as a consequence of elevation of land, the two different forms will then be maintained as distinct 'species'.

The case of the *Euploea doubledayi*-complex presents an instructive example of this phenomenon in Malaya. In the large and dark Burmese form of *E. doubledayi* C. & R. Feld., the female has white discal spots on the forewing, while the Malaysian form *eyndhovii* C. & R. Feld., flying in Malaya, Sumatra, Borneo and Java, is smaller and paler brown with the female forewing not spotted as in Burma. Were these the only forms of the *E. doubledayi*-complex in this part of the distribution area, a systematist would have no hesitation in placing them as geographical races of a single species. In Malaya, however, is a second form, *evalida* (Swinh.), whose affinities are with the Burmese form. There is little doubt that *evalida* is a comparatively recent offshoot of the Burmese *doubledayi*, for it is most abundant in northern Malaya, becomes progressively rarer on proceeding south and is not yet known from the southern half of the Peninsula. On the other hand, the smaller Malaysian *eyndhovii* is equally abundant throughout the Peninsula.

As a further example of overlapping Malayan species, the *Euthalia cocythus-godartii* complex may be cited. The difference between the two *Euthalia* species is more marked than is the case with the *Euploea* species, although the evidence suggests that they comprised a single species in the not very remote past. *E. cocythus* (F.) is confined to Burma and the northern states of Malaya, while *E. godartii* (G. R. Gray) is a truly Malaysian species found in Malaya, Sumatra, Borneo and Java, and it has extended its range northwards so that it now overlaps *E. cocythus* in northern Malaya, Peninsular Siam and south Burma.

Borneo also appears to possess a number of such duplex species and the curious polymorphism found in this island in other *Rhopaloceros* genera besides *Tanaëcia* may be the result of isolated races meeting and interbreeding before they have advanced too far along the road to specific isolation.

Perhaps enough has been said to show how complicated is this problem of assessing the importance of faunistic boundary lines in the Archipelago.



In the writer's opinion, it is preferable to divide this area into a number of more or less clearly defined subregions rather than to press the lines of Wallace and Weber too far.

The division of subregions given below has proved satisfactory, as far as the Rhopalocera are concerned, for Malaysia, Philippines and the Celebes, but much work remains to be done regarding the distribution of the insect fauna of the eastern part of the Archipelago. It appears probable that a dividing line should be placed between Alor and Timor in the rather heterogeneous group of Lesser Sunda Islands.

The subregions are :—

**MALAYSIA**, comprising Malaya, Sumatra, Borneo, Java, Bali, Palawan and the satellite islands off the west coast of Sumatra.

**PHILIPPINES**, exclusive of Palawan.

**CELEBES**.

**MOLUCCAS AND NEW GUINEA**.

**LESSER SUNDA ISLANDS**, consisting of the islands from Lombok to Tenimber.

## THE BIOGEOGRAPHIC DIVISION OF THE INDO-AUSTRALIAN ARCHIPELAGO : 5. SOME GENERAL CONSIDERATIONS FROM THE BOTANICAL STANDPOINT.

By H. K. AIRY SHAW.

In his 'Report of a botanical trip to the Ranau region', southern Sumatra, van Steenis (1933) emphasizes the important fact, already brought out by Schröter (1909) for the Canaries and by Skottsberg (1930) for Hawaii, that the lowland flora and the mountain flora of a region may not necessarily show the same affinities, i.e., that of these two altitudinally distinct components or 'layers' of the flora of a given area, one may have its main affinities, say, to the west, the other to the east.

The case in point was the flora of the western Malaysian area. To quote van Steenis's own words, 'the lowland flora of Sumatra is definitely allied with that of Borneo, the Malay Peninsula and the Philippines, and *not* to that of Java' (loc. cit. p. 28). But, 'whereas the lowland flora of Sumatra is closely allied to that of Borneo, the Sumatran mountain flora differs greatly from the Bornean one and is almost identical with that of Java' (loc. cit. p. 36). The importance of this conclusion for our purpose can hardly be overrated, since it is immediately evident that any biogeographic division which is valid for the lowland flora may be inapplicable to the mountain flora, and *vice versa*. Van Steenis summarizes the position thus (loc. cit. p. 37) :—

1. The lowland forests of Sumatra, the Malay Peninsula, Borneo and the Philippines show a very close affinity, the typical representatives of which do not occur in Java and the Lesser Sunda Islands.

2. The mountain floras of Sumatra and Java and the Lesser Sunda Islands are closely allied with each other and must have got their elements

from the Himalayan region ; it differs entirely from the Bornean mountain flora. A similar contrast in alliance of mountain and lowland flora is indicated to exist in the Philippines, Hawaii and the Canaries.

3. It follows from 1 and 2 that in phytogeographical discussions it is not permitted to mix up lowland and mountain plants ; these two categories may show different affinities in one island or region and their affinity must be examined separately.'

Botanists must, therefore, clearly state whether the evidence which they may offer, relating to biogeographic divisions, is based upon the lowland flora, upon the mountain flora, or upon a mixture of the two. While it is, no doubt, the lowland flora that will generally be utilized (because usually the predominant element), it is probable that, when we know more concerning the various elements of which the lowland and mountain floras are composed, especially as regards their probable places, dates and modes of origin, we shall find it necessary to recognize several different, superimposed, biogeographic divisions, according to the several geological ages of the elements under consideration.

Palaeoclimatology, though necessarily to some extent speculative, but in so far as it may be reliable, should increasingly throw light on anomalies of distribution. Past climatic vicissitudes are certain to be reflected in some degree in the present composition of flora and fauna. Merrill (1926, p. 133) writes : 'Geologists are in agreement that the Cretaceous was a period of remarkable climatic uniformity, in which the strictly tropical types of vegetation extended far to the north and to the south'. Since that period, climatic fluctuations in most parts of the earth appear to have been many and varied. The vegetation of the earth as we know it today is the result of the action and interaction of a complex series of changes, in which the original relatively uniform climate of the late Mesozoic, which saw the Angiosperms rise to dominance, has become replaced by a progressively more and more strongly differentiated climatic zonation : and in which, as seems now almost certain through the work of Wegener and others, very great cleavages and lateral displacements of the continental blocks have occurred, as well as, possibly, secular shifts of the poles and equator, as Kreichgauer, for instance, has claimed. The extensive folding caused by the continental displacements in many parts of the earth has resulted in the creation of great mountain systems, which, in their turn, have produced profound local modifications of climate, for example through altering the distribution of rainfall or through acting as centres of glaciation. The alternate formation and dispersal of large ice-caps have caused a corresponding lowering and raising of the level of the sea and the sea's consequent retreat from and advance over many relatively level, low-lying, continental shelves. The existing flora is, therefore, composed of at least (a) an ancient, more or less original, perhaps Cretaceous (or even earlier) element, now consisting mostly of relict forms ; (b) an extensive mesophil, lowland flora, consisting of many superposed layers of later 'infiltrations' from various directions, conditioned mainly, in an archipelagic region such as Malaysia, by the existence or otherwise of the necessary land-connections and hence having possibly taken place principally during glacial epochs when the

sea-level was appreciably lowered; conditioned also by the secular stability or constancy of the climate of the region since their arrival; (c) numerous reductive forms occurring in more specialized habitats, such as high mountains, deserts, streams, etc., and exhibiting various types of adaptation and specialization, derived mainly from (b) as autochthonous products, and called into being in direct response to the changes of climate or topography mentioned above.

Lam (1934, p. 124) recognizes three elements which he describes as follows:—

1. relic-endemisms, being the progeny of unknown elements or of plants that have immigrated a long time ago;
2. neo-endemisms, being the offspring of plants which have immigrated in more recent times;
3. recent immigrants, which have not, or not yet, had the opportunity or the time to raise new species and for which the country thus forms a part of their area.'

Again, Lam writes (loc. cit.): 'While the *vegetation* is mainly a function of the external factors and only in the second place of time, the last-named factor plays a prominent part regarding the *flora*. . . . Time and immigration possibilities are . . . the main factors that determine a flora; ecological conditions, however important and selective they may be, are second in rank.'

I believe that botanists would be more usefully employed in the admittedly difficult task of trying to segregate, or sort out, the known components of the flora into their probable elements, and in collecting all available information towards this end, than in attempting any biogeographical division of the region at present.

But if any division is to be made, then it should be based, *primarily*, upon broad considerations of geology, ecology and climate, and only *secondarily* upon the observed distributional characteristics of individual taxonomic groups. Our knowledge of the detailed composition of the flora and of the detailed distribution of its components is still so imperfect, and is bound for long to remain so, whereas our knowledge of the gross features of the vegetation and climate is naturally far more complete. In an area such as Malaysia, in which large areas (e.g. of Sumatra, Borneo, Celebes, New Guinea, etc.) are quite unexplored, any other method would seem premature, because too much subject to modification with every fresh fact of distribution that comes to light. I may point out, too, that the Herbarium representation, in Great Britain, of the important central area comprising Celebes and the Moluccas, besides most of the Lesser Sunda Islands, is either extremely scanty, or almost negligible, and quite inadequate for drawing reliable phytogeographical conclusions. We can only take our data second-hand from Dutch and American workers, which is, of course, unsatisfactory—and this is no reflection upon the excellence of their work.

The geology, as I understand it, indicates two relatively stable areas—Sunda-land and Sahul-land—and an intermediate unstable area—Wallacea. The climate and ecology agree in indicating (1) an extensive region characterized by tropical rain-forest and (except in the Moluccas)

large stretches of coastal mangroves; this corresponds closely to the equatorial belt where the 29.8-29.9-inch (757-758 mm.) isobars remain more or less constant throughout the year, and where there is consequently an even annual distribution of rainfall; (2) a much smaller area, influenced by the 'continental' of the Australian land-mass, characterized by the presence of mixed deciduous 'monsoon' forest, *Eucalyptus*, (*Asuarina* or teak forest, and palm-savannahs (van Steenis, 1935 b, 1938). This latter area comprises Java (except the extreme west) and the Lesser Sunda Islands (except perhaps the Tenimber and Kei Islands), together with the southern half of the south-western peninsula of Celebes; it also corresponds closely with the area having a pronounced dry season, with fewer than 20 rainy days in the driest four months of the year (cf. Lam, 1934, p. 122), and with the area having an 'oceanity' index of less than 250, as determined by F. Rosenkrantz's method (1937, p. 285). Rosenkrantz's formula, which attempts to integrate the factors of annual rainfall, relative humidity, and mean temperature, takes no account of barometer constancy, and might well give a still more accurate result if distribution of rainfall, instead of, or at least as well as, total annual rainfall, were utilized.

Area (1) would then be subdivided into two portions, a Western and an Eastern, by the Macassar Straits. The floristic gulf between Borneo and Celebes seems beyond dispute. The important Dipterocarp element in the primary forests of the Philippines suggests that these islands should be associated with the western portion in a phytogeographical scheme, unless they be constituted a separate subdivision. The latter course would perhaps in fact be best, in view of the very considerable affinities shown by certain other elements in the Philippine flora with Celebes, the Moluccas and New Guinea (cf. Merrill, 1926, pp. 96-100). New Guinea, if only on account of its possible origin and floristic peculiarities, to which I shall allude later, would form a subdivision distinct from Celebes and the Moluccas, and would thus confirm the position of Lydekker's Line.

But before we can fully understand the biogeographic relationships of any region (or for that matter of the world) a great deal more work must be done on what one may term the probable evolutionary dynamics of individual taxonomic groups. It is an aspect of the problem which appears to have received very little attention. An excellent example of the type of research which I have in mind is provided in a paper by V. I. Krechetovich, the well-known Soviet caricologist, entitled 'Are the sedges of the subgenus *Primocarex* Kük. primitive?' (Krechetovich, 1936). It was brought to my notice last year by my colleague, Mr. E. Nelves. I trust I may be forgiven for a short and, I hope, not wholly irrelevant digression on this subject.

Krechetovich's—as it seems to me—rather noteworthy piece of research deserves, on account of its wider implications, to be more widely known amongst botanists and especially amongst phytogeographers. He has shown, in a manner which, as far as my limited geological knowledge permits me to judge, seems in its main features convincing, that the members of Kükenthal's first subgenus, *Primocarex*, so far from representing 'primitive' types, as Kükenthal claimed, are in reality much



reduced forms, and that their reduction and present distribution can be traced to the effect of (a) glacial periods, (b) mountain-forming processes, (c) changes in the position of the equator. Each change of climate and environment, resulting from these three major causes, left its own distinctive impression on different groups of sedges, in the shape of various types of structural change, all in the direction of reduction or simplification. Obviously it would be out of place to go into details here; the main point is that Krechetovich has brought out clearly the possibility of establishing a correlation between plant-structure and distribution and past geological and climatic changes.

Now, while it is probable that the genus *Carex*, owing to its large number of species and its occurrence in almost every part of the globe, presents exceptionally favourable opportunities for this type of investigation, it is equally probable that the comparative study, along these lines, of widely distributed groups such as the *Gramineae*, *Senecio*, *Juncus*, *Ranunculus*, and very many others, would produce almost equally valuable results. It is here, it seems to me, that a golden opportunity awaits the intelligent phylogenist (if you will forgive the apparent oxymoron), who will perhaps be surprised to discover that there is an increasing body of opinion which will welcome, and appreciate, such admittedly, in their first stages, speculative attempts—though he will of course be greeted with howls of derisive abuse in certain other quarters. I venture to suggest, however, that Krechetovich's work has put such investigations beyond the realm of pure speculation and brought it well within the scope of orthodox, 'respectable' botany, and I commend its study to all who are interested in phytogeography.

Lastly, I would like to make an appeal for more information from geologists and palaeoclimatologists. First, as regards the Ice Age. The extent and effects of the last glaciation in the northern hemisphere, especially in Europe and North America, appear to be well established. Its effects in the tropics, however, appear to have been relatively slight, except in so far as alterations in the sea-level may have been concerned. What is the present state of our knowledge on this subject?

Secondly, as regards past changes in the position of the equator. If, as astronomers apparently maintain, 'it is very unlikely that the position of the poles (i.e. of the earth's axis) has materially changed in the course of geological time' (van Steenis, 1935 a, p. 392), then the apparent shifting of the equator during geological time, as indicated by fossil records, must be entirely due to drifting of the earth's crust, as demanded by the displacement theory of Wegener. But Köppen and Wegener, in their book 'Die Klimate der geologischen Vorzeit' (1924), produce such a variety of evidence, all apparently harmonizing remarkably well, in favour of polar wandering, as they term it, that this conclusion seems difficult to avoid. These authors even go so far as to say: 'The wandering of the poles is . . . no longer a hypothesis but an empirically established fact. For the zonal distribution of dry and humid regions excludes any other explanation' (1924, p. 4).

It is perhaps worth remembering that, as Sir George C. Simpson (1931) has pointed out, 'Wegener was a mathematician and astronomer before he became a meteorologist, and therefore was quite familiar with the

mechanics of a spinning body', when putting forward his views on polar shift. (See, however, Du Toit (1937), chap. xiii, especially pp. 270-2, 288-9.)

Köppen and Wegener (1924) and Kreichgauer (1925) agree that the Malaysian region has remained practically wholly within the tropical zone from the Cretaceous onwards, but the former authors claim that as recently as the early Quaternary the southern part of it came under the tropics of Capricorn. Is this regarded as well-established? If so, is it possible that the different aspect of the vegetation of the southern fringe of the Archipelago, from Java to Timor, may be *partly* due to this cause?

Thirdly, as regards one of Wegener's more remarkable claims, with important bearings for the biogeography of Malaysia, to which Lam (1934, pp. 141-4) has given renewed attention. I refer to the supposed movement of the Australia-New Guinea continental block, from a position in the Antarctic, northwards, till it collided with, deformed, and partly broke through, the eastern part of the Malay Archipelago. The depth chart published on p. 67 of the English edition (1924) of Wegener's book, and still more so the remarkable map of the Malay orogens reproduced by Lam (*loc. cit.* p. 143) from Smit Sibinga (1933), certainly give strong colour to this startling hypothesis. I should like to know what is the general attitude of geologists to this question. Lam says that he 'cannot help apologizing for the above, fairly bold and perhaps somewhat premature, conception' (*loc. cit.* p. 144), and perhaps therefore I ought to do the same for referring to it here. But if there is any likelihood of probability or even possibility in the theory, it should be given the closest consideration, however bold and apparently premature it may seem. Lam believes that the high degree of specific differentiation in the New Guinea flora, as compared with that in the Bornean flora (proportion of species to family over two and a half times as great in New Guinea as in Borneo), may be attributed to the migration (after the establishment of the necessary land-contact) of a rich tropical flora from Malaya into a 'recently arrived' area with a relatively much poorer subtemperate flora, and there undergoing great evolutionary development; running amok, as it were, in the absence of effective competition. The generic endemism of New Guinea is nearly three times as great as that of Borneo, a fact which points in the same direction.

It may be that I am unduly under the spell of Wegener; if so, I hope that I may be pardoned, since I cannot entirely suppress a certain clannish sense of satisfaction that the first germs of the theory of isostatic compensation, or flotation of the earth's crust, upon which Wegener's theory so largely depends for its feasibility, were originally suggested, in 1855, by my great-grandfather (Airy, 1855; cf. Hinks, 1931). I firmly believe, however, that Wegener's hypothesis, or extensions or modifications of it, will ultimately give us the clue to much that seems at present inexplicable in the distribution of plants and animals.

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## THE BIOGEOGRAPHIC DIVISION OF THE INDO-AUSTRALIAN ARCHIPELAGO: 6. THE ECOLOGICAL SEGREGATION OF THE INDO-MALAYAN AND AUSTRALIAN ELEMENTS IN THE VEGETATION OF BORNEO.

By P. W. RICHARDS, Ph.D., F.L.S.

THE flora of the Malayan region is so rich and still so imperfectly known that it is difficult to generalize about its geography, even with a life-time's experience. As my only first-hand experience of it is a few months' field-work in Borneo, chiefly on and about the mountain range of Gunong Dulit in northern Sarawak, I join in this discussion with some hesitation.

I went to Borneo to study plant communities and I was interested in the vegetation more as an ecologist than as a taxonomist or plant-geographer. Looking at it from this point of view, I was much struck by certain facts which seem to me to have an important bearing on the subject now under discussion.

The point I particularly wish to emphasize—and no doubt much the same is true of other parts of the Malayan region—is that in Borneo elements in the flora of different geographical origin show a very marked tendency to be segregated into different habitats. To a first approximation we can regard the flora of Borneo as consisting of two chief components, a dominant Indo-Malayan one, which has reached Borneo from the west, and a less conspicuous Australian element which has certainly come from the south-east. The Mixed Evergreen Rain-forest, which forms the bulk of the lowland vegetation, consists almost exclusively of the Indo-Malayan element, while the Australian element is found, in the first place, in the dwarfe and less shady 'mossy forest', or montane rain-forest, which covers the mountain ridges above about 3,000 feet, and secondly, to a much smaller extent, in a number of special lowland habitats which I shall mention in a moment—all of them characterized by comparatively open vegetation and the absence of very intense shade.



The Indo-Malayan flora is thus associated with dense evergreen forest casting a deep shade, the Australian with lighter and more open conditions. These facts are not altogether new, but I do not think their importance has been fully realized.

If one climbs the steep scarp face of Gunong Dulit, one passes quite abruptly, at a height varying from 3,000-3,700 feet, from more or less tall rain-forest into the very different and much less shady 'mossy forest', where the most striking feature is the luxuriant covering of liverworts and mosses which conceals the trunks and branches. In the tall rain-forest, up to a height of at least 1,500 feet, the dominant family of trees is the characteristically Indo-Malayan Dipterocarpaceae, above that height the families are more mixed, but throughout its altitudinal range, the lowland rain-forest is composed, as far as I am aware, almost entirely of species of Indo-Malayan origin. In the 'mossy forest' the state of affairs is quite different: though there, too, the majority of the species is probably Indo-Malayan, a very considerable minority, including some of the commonest and most conspicuous trees, is Australian. Thus, among the trees there are a species of *Casuarina*, species of *Weinmannia* and *Tristania*, three species of *Dacrydium* and a *Phyllocladus*. In addition to the trees there are the shrubs *Drimys Piperita*, *Leptospermum javanicum* and *Styphelia malayana*, all of which belong to Australian groups. These are only a few examples, and this abundance of Australian elements in the montane rain-forest is by no means peculiar to Gunong Dulit: it is characteristic of all the mountains of Borneo, indeed, I believe, of the mountains of the Malayan region generally. On Kinabalu, in British North Borneo, it is even more marked, as Stapf showed long ago.

As already mentioned, the Australian elements are not all upland, some also occurring in certain special and localized lowland habitats. The first of these is the beach forest of sandy sea-shores, where we have, for instance, *Casuarina equisetifolia* and *Scaevola Koenigii*—both clearly of Australian affinities, though themselves widely distributed. A second habitat of Australian elements is the peat-swamps—which I do not myself know at first hand—where *Melaleuca Leucadendron*, belonging to an almost exclusively Australian genus, is often abundant or even dominant. Finally, there are two more lowland-plant communities where Australian elements may be found, the so-called *padangs* and the 'Heath Forest' or *Heidewald*. The *padangs* are open stretches of low, heath-like vegetation found on very sterile porous soils which, as H. J. Hardon (Proc. Roy. Acad. Sci. Amst. Afd. Naturk. (2de sectie), xxx, 1-85, iii, 1933) has recently shown, resemble the podsols of temperate climates. *Padangs* are widespread in the lowlands of Borneo and occur also in Bangka and elsewhere in the Archipelago. The 'Heath Forest' (like the *padangs* rather unfortunately named) is found on a sandy soil very like that of the *padangs*; it is a type of tall evergreen rain-forest differing from the normal lowland rain-forest in floristic composition and in the better illumination of the undergrowth. Both the *padangs* and the 'Heath Forest' are the home of a number of Australian elements. In the *padangs* these are *Baeckea frutescens*, *Casuarina sumatrana*, *Styphelia malayana*, *Leptospermum flavescens* and probably others. In the 'Heath Forest', though the Indo-Malayan Dipterocarps are still generally the



dominant family, several of the common trees belong to Australian genera, for instance *Agathis borneensis*, *Casuarina sumatrana*, *Tristania* species, and doubtless others not yet recognized. In some parts of Borneo the Conifer *Dacrydium elatum*, again an Australian type, is abundant in the 'Heath Forest': on the Lawas River in the north of Sarawak it grows in a nearly pure stand.

All these habitats of Australian elements—the 'mossy forest', the beach forest, the 'Heath Forest', the *padangs* and probably the *Melaleuca* swamps—have a relatively poor, sandy soil, and, doubtless as a consequence of this, relatively open vegetation not casting a deep shade. It is evident that the Australian elements are adapted to a different set of conditions to the Indo-Malayan elements, and have only penetrated northwards where local conditions happened to suit them.

If we turn to eastern Australia, for instance to the coast of New South Wales, we see the same picture reversed. As Prof. Herbert, Prof. Osborn and others have emphasized, there are the same two elements in the vegetation, an Indo-Malayan one and an endemic Australian one; and, as in Borneo, the two are segregated into different habitats, the Indo-Malayan elements being confined to the shady evergreen rain-forest which occurs on the more fertile soils, especially in moist sheltered valleys, while the Australian flora is found in the more open Eucalypt forests and sclerophyll scrub which occur on the poorer soils and in less sheltered situations. I call this picture reversed, because here it is the rain-forest vegetation which occupies the limited habitats and the Australian vegetation which is widespread, while in Borneo, the rain-forest covers a wide area and the Australian elements a restricted one.

What, then, is the bearing of this on Wallace's Line and the other proposed dividing lines in the Malayan region? If the Indo-Malayan and Australian components of the vegetation are adapted, as they certainly seem to be, to different complexes of conditions, it follows that their distribution over the Malayan islands will be determined as much by the present distribution of these conditions as by historical factors, such as former land-bridges. In so far as Wallace's Line and the other lines hold at all for plants, I suggest that they do so because they happen to correspond to some extent to climatic boundaries determining the general character of the environment and the vegetation. Thus Wallace's Line has a rough correspondence with the boundary between the western part of the Archipelago with a continually moist climate, and the eastern part in which the seasonal drought due to the SE. monsoon begins to be felt. Certain elements in the flora extend as far east, or as far west, as Wallace's Line because the conditions to which they are adapted do the same.

Whether these ideas have any application to animals I do not know, but I cannot help feeling that a thorough study of the ecology of the Malayan fauna might show rather similar relations to hold.

# THE BIOGEOGRAPHIC DIVISION OF THE INDO-AUSTRALIAN ARCHIPELAGO: 7. THE DIVISIONS AS INDICATED BY THE DISTRIBUTION OF INSECTS IN RELATION TO GEOLOGY.

By F. E. ZEUNER, D.Sc., F.G.S., F.Z.S.

THE problem under discussion is that of delimiting the Oriental and Australian regions which, on the Asiatic and Australian continents respectively, are perfectly distinct but merge into one another in the Indo-Australian Archipelago. Since Wallace's time it has been known that this transition is not entirely gradual and not merely proportional to the distance of either Asia or Australia, and two more or less clearly defined lines have been constructed east of which the fauna, taken as a whole, has a more decidedly Australian, and less decidedly Asiatic, aspect than west of it. These are the Wallace line and the Weber line. They have suffered much criticism almost from the moment when each of them was put forward for the first time.

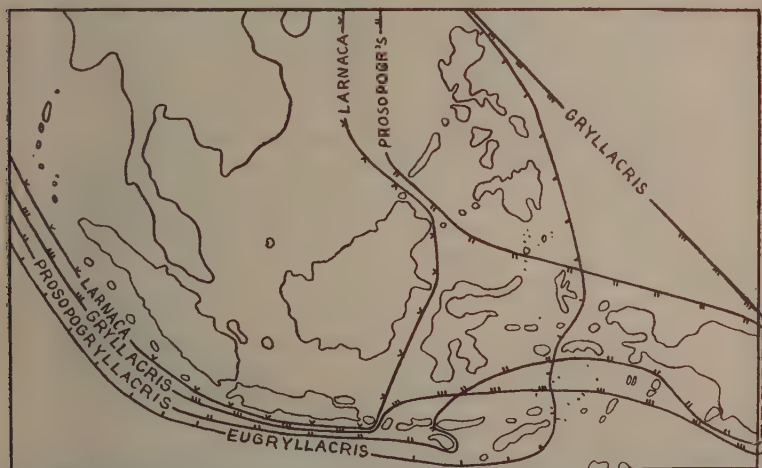


FIG. 1.—Advance of Asiatic elements, exemplified by genera of the Gryllacrididae (Orthoptera Ensifera): *Larnaca* Walker (8 species), *Gryllacris* Serville (35 species), *Prosopogryllacris* Karny (13 species), *Eugryllacris* Karny (16 species).

The proposed lines and their varieties are intended to serve as dividing lines in biogeography, and it has consequently been assumed that they are universally applicable. It has been found, however, that only a minority of species and genera reach the limits of their areas along one of the variants of these lines, and that the number of such species and genera varies considerably with the group examined. The value of suggesting any such lines has, therefore, been questioned.

Whilst all workers now agree that the Wallace and Weber lines are not, and cannot be, sharp faunal boundaries such as that afforded, for

instance, by the Atlantic Ocean between Africa and South America, the fact that they do apply in some groups and not in others calls for an explanation.

The present-day distribution of land and sea does not provide a satisfactory solution of the problems involved in the distribution of insects in the Archipelago. The present climate of parts of the area provides a limiting factor (see p. 162), but it cannot explain, for instance, the difference between the faunas of Borneo and Celebes. The history of the Archipelago, therefore, is likely to contain the clue.

Fossil evidence not being available in the case of Australasian insects, an examination of certain types of distribution has to be made use of in elucidating the problem.

Fig. 1 illustrates a few instances of genera, taken from the Gryllacrididae (Orth. Salt.). Whilst *Larnaca* Walker conforms to the Wallace line (though not yet known from either Palawan or the Philippines), *Gryllacris*

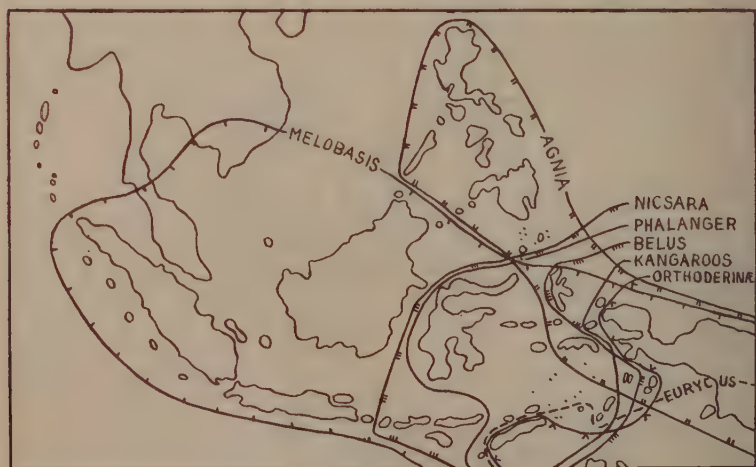


FIG. 2.—Advance of Australian elements, exemplified by *Eurycus* Boisduval (one species, Lepidoptera Papilionidae), Orthoderinae (2 genera, 9 species, Mantodea), Kangaroos (many species, Marsupialia), *Belus* Schoenherr (70 species, Coleoptera Curculionidae), *Phalanger* Storr (5 species, Marsupialia), *Nicsara* Walker (20 species, Orthoptera Salomoninae), *Agnia* Newm. (7 species, Coleoptera Cerambycidae), *Melobasis* Cast. (about 100 species, Coleoptera Buprestidae).

Serville has spread across Celebes and the Moluccas to New Guinea and the Papuan subregion without, however, occupying the Lesser Sunda Isles. *Prosopogryllacris* Karny differs from *Gryllacris* in not having occupied the Philippines and in having advanced to Flores and Sumba. A third type of distribution is represented by *Eugryllacris* Karny, which has advanced with a broad front to Timor, Halmahera and the Philippines. These examples could easily be multiplied; they show that strict adherence of genera to the Wallace and Weber lines is the exception rather than the rule.

The dispersal of some Australian genera, subfamilies and families (two of them taken from the Marsupialia) is illustrated by fig. 2. Here it is found that certain genera, subfamilies or families (*Eurycus* Boisduval, sole species *E. cressida* F., Lep. Pap.: Orthoderinae, Orth. Mant.; Kangaroos, Marsupialia: *Belus* Schoenherr, Col. Curc.) conform more or less well to one of the varieties of the Weber line, whilst others have spread to the Philippines (*Agnia* Newm., Col. Ceramb.), Celebes (*Niesara* Walker, Orth. Tett., which has reached, but not crossed, the Wallace line as defined by Wallace: *Phalanger* Storr, Marsupialia) and even the Asiatic continent (*Melobasis* Cast., Col. Buprest.). Of the Lesser Sunda Isles, Timor has received a comparatively large number of Australian elements, but other instances (*Phalanger*) suggest that at least some groups find it difficult to spread along the Lesser Sunda chain. This applies to both directions, and to certain plants also, as exemplified by Mr. Burkill and other speakers in this discussion.

Of genera and higher taxonomic units it may be said that they often do not conform to the Wallace or Weber lines. The genera which do most frequently, contain a few, or even one, species only (*Eurycus*, Orthoderinae). An exception is *Belus* Schoenh., with about 70 species.

If, however, the distribution of species and subspecies is examined, the Wallace and Weber lines prove to be of relatively greater significance. As an instance, the distribution of the Malayan species of *Arhopala* Boisd. (Lep. Lye.), a genus which has recently been revised by Dr. Corbet, may be quoted. In this context it does not matter how far the species have penetrated into Burma, India and China. If one classifies them according to the tendency to cross the Wallace line, one finds that

78 species occur in Sundaland and Palawan, but not east of the Wallace line as defined by Huxley;

10 species are found in the Philippines also, but not east of the Wallace line as defined by Wallace;

7 species have crossed the Wallace line and are found on islands in the deep-sea portion of the Archipelago, in the Papuan sub-region and Australia.

The present distribution of insects (and mammals) thus appears to support the following conclusions:—

(1) The great differences in the faunas of the continental portions of Asia and Australia indicate that these faunas developed independently for some considerable time in the remote past.

(2) The type of distribution of Australian and Asiatic genera over the Indo-Australian island zone suggests that contact between the two regions must have been established at a date sufficiently remote to allow of immigrant groups to produce many new species and even genera.

(3) The restriction of a comparatively large number of species to the areas west of the Wallace line and east of the Weber line indicates that the dispersal of these species was rendered difficult or impossible in comparatively recent times.

(4) There was, and apparently still is, some obstacle preventing many species and genera from spreading along the Lesser Sunda chain.



These points are readily interpreted in the light of the geological history of the Archipelago. Point (1) is substantiated by the fact that most islands between the continental shelves of Asia (Sundaland) and Australia (Sahul Shelf) did not exist before the Tertiary, and probably the upper Tertiary. Moreover, many adherents of the theory of continental drift claim that Australia + New Guinea have, during the Tertiary and Pleistocene, moved into their present position from further south. The Australian fauna, therefore, can have had little contact with the Asiatic fauna before the islands of the Archipelago began to afford stepping stones for dispersal.

Point (2) is explained by the geological fact that many islands were above sea-level in the upper Tertiary, so that the exchange of faunal elements began long before the Pleistocene period.

Point (3), the restriction of many species to the shelf areas appears to be connected with the fluctuations of the sea-level during the Pleistocene. These fluctuations, the importance of which has been emphasized by Mr. Scrivenor, had a maximum range between +100 m. and -200 m. When the sea-level was low (see Zeuner, 1942, fig. 2, or 1943, fig. 114), the larger Sunda Isles formed that well-known extension of the Asiatic continent called Sundaland, which is now the home of the Malaysian fauna, but there never existed a land-connection between Bali and Lombok, Borneo and the Jolo Isles, Palawan and Mindoro. This explains the homogeneity of the Malaysian fauna as compared with the faunas of the islands of the deep sea to the east. It also suggests a course for the Wallace line based on the geological history of the area. It is identical with the Wallace line as originally proposed by Huxley.

On the Australian side, New Guinea and the Aru Isles were connected with Australia during the phases of Pleistocene low sea-level by the extensive Sahul Shelf (350 miles of land added to Western Australia in the direction of Timor; remaining gap 70 miles). Here, conditions resembled, *mutatis mutandis*, those prevailing along the Wallace line, and a course is suggested for the Weber line as running along the edge of the Sahul Shelf.

#### GEOLOGICAL DEFINITION OF WALLACE AND WEBER LINES.

The numerous attempts at laying down boundary lines based on biological data alone have shown that uniformity in the divisions is not attainable in this way. Since the faunal distribution is indubitably the outcome of the peculiar geological past of the Archipelago, I venture to suggest that the main geological features, which are the source of the phenomena observed, be used in order to define the Wallace and Weber lines. In other words, they should be identified with the edges of the continental shelves (depth-lines of 100 fathom or 200 m.) of Sundaland (Wallace line) and Sahul Shelf (Weber line).

Alternative ways of defining on a geological basis the Wallace and Weber lines are afforded by structural differences. The Sahul and Sundaland shelves consist mainly of consolidated rocks of great age, and they have not been affected by the Tertiary folding processes which produced the islands of the deep sea between Asia and Australia. If one accepted the boundaries of these old blocks as biogeographical dividing

lines, the mountains of western Sumatra, nearly all of Java, a large portion of Borneo, and the whole of New Guinea except the south would have to be included in the transitional area. Though a few instances of recent distribution of insects and, as I gather from Dr. Shaw's contribution, of plants also, do support this alternative, it would be impracticable to draw dividing lines lengthwise through Sumatra and New Guinea.

Other structural boundaries which might be considered as substitutes for the biological variants of the Weber line are the alignments of volcanoes and the close and parallel zone of negative anomaly of gravity.

A line of active volcanoes occupies the inner arc of the Sunda Isles from Sumatra to Banda: another line follows the west coast of Halmahera; and a third commences on the Minahassa and continues into the Philippines. Since biogeographical boundaries in the Archipelago should, wherever possible, be drawn in the sea between the islands, the alignments of volcanoes are unsuitable, although they, too, are a product of the causes which resulted in the differentiation of biogeographical regions and subregions. For the same reason the zone of gravity anomaly cannot be used; though it lies south of Sumatra and the isles as far as Sumba, and though it separates Celebes from Halmahera, it runs *across* Timor, Tenimber and Ceram.

As a last alternative basis for boundary lines, the deep ocean troughs and basins have to be mentioned, since they have been used by Boden Kloss in his attempt at fixing the zoogeographical boundaries in the Archipelago. The dynamic interpretation of these troughs and hollows is still under discussion, but geologists will agree that the troughs south of the Sunda Isles and the deep basin of the Banda Sea between Tenimber, Kei and Banda, are not parts of the same geological unit. The Philippine trough may be a homologue of the Java trough. These three depressions of the bottom of the ocean were combined by Boden Kloss to demarcate the Weber line. Terrestrial faunas, however, are not concerned with the depth of the water, provided it is greater than about 100 fathoms which have to be allowed for oscillations of the sea-level during the Pleistocene. There is no justification in preferring the very deep parts of the ocean to the less deep ones for the purpose of establishing biogeographical boundaries, unless one regards them simply as a geological feature.

Having the choice of several geological features, some of which (volcanoes, gravity anomaly, boundaries of consolidated blocks, deep sea troughs) are only indirectly connected with the phenomena of faunal dispersal and one (the continental shelves) which has actually played a great part in the differentiation of subregions in the near past, one has no hesitation in accepting the latter as a geological basis for faunal boundaries. If the edges of the continental shelves are accepted as boundaries for the Malaysian subregion in the west and the Australian region in the east, the question arises of what the transitional zone of deep sea islands should be assigned to as a subregion. This zone, from the Philippines in the north to the Lesser Sunda Isles in the south, is best called the Austro-Oriental subregion. Being geologically the outpost of Asia and, faunally much more Asiatic than Australian (except near its eastern fringe), it should be attached to the Oriental region.

It is, of course, necessary to subdivide the Austro-Oriental subregion into the Philippine, Celebian, Moluccan and Lesser Sunda (or Timorese) subregions. These subunits are distinguished from one another by their geological history.

Finally, point (4) requires brief consideration. The chains of the Lesser Sunda Isles are geologically very young. Except perhaps for a few older cores (Timor, for instance), they were beneath sea-level during most of the late Tertiary, and still, or once more, almost entirely submerged at the beginning of the Pleistocene. There was little opportunity for using this dispersal route previous to the Pleistocene.

The second factor which, in my opinion, bars many species from the Lesser Sunda Isles is their climate. This climatic aspect of the composition of the Lesser Sunda fauna first attracted the attention of Setchell in 1930. From east Java eastwards, a marked dry season occurs, and many forms adapted to the equatorial belt of rain forest are probably unable to persist in those islands. The equatorial belt of rain all the year round extends from the Malay Peninsula and Sumatra through Borneo, Celebes, the Moluccas to New Guinea, and it is this dispersal route to which rain-forest elements are confined. It is my impression that the existence since Pleistocene times of two dispersal routes with a different climate and, consequently, used by different faunal elements, has considerably obscured the theoretically expected picture of the Asiatic and Australian faunas advancing eastwards and westwards with broad fronts stretching from north to south.

### *Summary.*

Summarizing, it appears that the present distribution of faunal elements in the Indo-Australian Archipelago is due to the interference of two phenomena:—

(1) The approach of two previously separated regions and their connection by island chains which are geologically much younger than the continental areas in which the faunas evolved their characteristics. Theoretically, this process would have favoured a meridional gradation in the composition of the fauna of its transitional zone.

(2) The existence of latitudinal climatic belts, which favours a latitudinal gradation in the composition of the fauna of the transitional zone.

It is evidently very difficult, if not impossible, to arrive at a generally acceptable biological definition of boundary lines for the faunal regions. If such boundary lines cannot be avoided, historical, i.e. geological, definitions, as suggested in this paper, are to be preferred.

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### Discussion.—

Mr. J. R. NORMAN pointed out that, as far as the true freshwater fishes are concerned, Wallace's line provides an almost perfect boundary between the Indo-Malayan and the Australian regions, but that the first of these two regions must be extended to include at least the more southerly of the Philippine Islands (Mindanao, Palawan, etc.). He drew attention to the remarkable contrast between Borneo on the one hand, with numerous genera and species of Cyprinoids, Siluroids, Anabantoids, Ophiocephaloids and so on, and Celebes on the other, without a single indigenous true freshwater fish. Fishes which do occur in rivers and streams of Australia, New Guinea, and islands east of Wallace's Line are either archaic forms, formerly with a wide distribution, representatives of marine families which have secondarily entered fresh water, or forms with accessory breathing organs which enable them to live out of water for a considerable time and which are known to be carried about alive by the natives.

He also showed a map illustrating the distribution of the freshwater Eels (*Anguilla*) in this region, and indicated how this might be correlated with former distribution of land and sea.

Mr. SCRIVENOR said that he would attempt to reply to Mr. Airy Shaw's question about the general attitude of geologists towards Wegener's theory of continental drift. He thought it was felt that the theory explained so much that there was good reason for believing in it ; but, at the same time, it must be confessed that it rested on nothing more substantial than the possibility of land-areas fitting together if moved towards one another. No proof of the theory had yet been produced, and the speaker recalled a criticism of many years ago, when it was pointed out that although we had considerable knowledge of the land-surfaces our knowledge of the ocean beds was very slight. The extension of echo-sounding would remedy this deficiency. In thanking the Society for inviting him to open this discussion, Mr. Scrivenor said that there was a danger of geologists relying too much on biologists for proof of theories regarding previous distribution of land and sea, and possibly there was a danger of biologists relying too much on geologists. Co-operation was essential, but each must strive to find proofs.



Dr. G. P. BIDDER thought that Mr. Scrivenor went a little too far in saying that, except the complementary outlines of American and Eur-African shores, there is no evidence for the Wegener origin of the Atlantic. In 1923 Dr. Bidder pointed out in 'Nature' (p. 429) that according to Flinders Petrie's detailed survey ('Pyramids and Temples of Gizeh', 1885, pp. 11 and 41) the Pyramids have their important north and south lines pointing about  $5\frac{1}{2}$  minutes to the west of the present true north, error of construction being probably less than 12 seconds. Beneath this, 'Nature' printed a confirmatory letter from Sir W. M. Flinders Petrie, saying: 'The undoubted trend of the pyramids at 4600 B.C. was about  $5'$  west of the present pole. . . . The cause of a change of axis of about  $5''$  per century might be due to ocean currents or to earth deformation.'

The withershins rotation of Africa through  $5'5$ , if pivoted on the isthmus of Suez, would widen the Straits of Gibraltar by 3.7 miles. It is a small piece of evidence of which only a geophysicist can estimate the value, but it is a fragment of positive evidence against the immobility of continents.\*

Dr. F. E. ZEUNER said that he agreed with Mr. Scrivenor that no evidence has yet been produced which proves conclusively that the Drift Theory is correct. There is, however, plenty of geological evidence suggesting that horizontal displacement of portions of the earth's surface has taken, and is taking, place. There is a second group of evidence, biological, which can be more readily explained by accepting horizontal displacements, but it would be a mistake to think that for this reason the Theory of Continental Drift with all its geophysical implications is true. If we confine ourselves to accepting the evidence alone, we are unlikely to fall into the trap of seeing everything in the light of a theory.

\* The Nansen E. to W. drift of ice in the Arctic Ocean, with its grinding pressure on the whole north shore of Asia, must be responsible for a strong contra-clockwise couple on the continent, reinforced by currents of the Pacific and Indian Oceans. Europe, on the contrary, has a clockwise couple put on it by the Atlantic currents; of the opposing stresses on the African oceanic coasts, the greater length of coast has a clockwise drag upon it. It is tempting to the ignorant to see, in the Pyramid rotation, evidence that Asia has been pushed round by the Arctic ice and has towed Africa along with her; the stretching of the tow-rope being marked by the transverse cracks of the Persian Gulf, Red Sea, and (in another epoch) by the rifts of Palestine and E. Africa. On this hypothesis, Atlantic pressure on Spain, France, Great Britain and Norway is too great to allow Europe to yield altogether and the Ural Mountains mark the no man's land of compression between withershins Asia and clockwise Europe; while the Straits of Gibraltar, like the Red Sea, show where tension has overcome coherence.

Turning to the jig-saw: the line tangent to the two bights of Ivory Coast and Gold Coast is inclined about  $73^\circ$  to the meridian, and on the N. coast of Brazil the line tangent to the two capes E. of the Amazon about  $108^\circ$ —difference  $35^\circ$ . In Africa the line from Biafra Coast to the mouth of the Congo and Loandra runs  $166^\circ$  from the meridian and in Brazil the Pernambuco—Frio line is  $202^\circ$  E. of N.—difference  $36^\circ$ . Taking  $35^\circ$  as the relative rotation that must have taken place if these two coast-lines once coincided, this at the Pyramid rate would have been performed by Africa in two and a half million years (which is of the order of some of Wegener's chronology), but the swing of America about Alaska, portrayed by Wegener, involves a clockwise rotation of Brazil which would have caused the  $35^\circ$  divergence to be reached more quickly.—G. P. BIDDER, May 1942.

As regards the Indo-Australian Archipelago, there is good geological evidence suggesting that Australia approached Asia in the course of the upper Tertiary and the Pleistocene. Faunal and floral distribution in the Archipelago, on the other hand, suggest that the intermingling of Asiatic and Australian elements is a comparatively recent phenomenon. Geological and biological evidence, therefore, corroborate the fact of horizontal displacement, but this has nothing to do with the geophysical premises of Wegener's theory.

Dr. B. P. UVAROV: The present discussion has brought out a very important general point. It has been shown by various speakers that the present distribution of any group of plants and animals is due to (1) the geological history of the area; (2) its palaeo-climatic history; (3) the rate of evolution in the group; and (4) the mode and the rate of dispersal in the group. All these are dynamic processes, and it would be scarcely reasonable to expect that their results could be represented by static lines on a map. Nor could these lines be the same for different groups, and if they are drawn to fit the statistical majority of cases, the minority has to be ignored. Fixed lines may be required for museum, etc., purposes, but they must be frankly regarded as a convention and drawn as most convenient in practice.

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## PROCEEDINGS OF THE GENERAL MEETING

14 May 1942

Dr. E. S. RUSSELL, O.B.E., M.A., President,  
in the Chair

The Proceedings of the General Meeting held on Thursday, 30 April 1942 having been circulated, were taken as read and confirmed.

The following Resolution conveying a message of congratulation to Svenska Linné-Sällskapet was read and passed by show of hands,—

THE Fellows of The Linnean Society of London in General Meeting assembled send greetings and congratulations to the Fellows of SVENSKA LINNÉ-SÄLLSKAPET on the twenty-fifth anniversary of the founding of that Society; and express the hope that, as in the past, the Society may continue to flourish.

Not only by the publication of its *Ärsskrift*, in which have appeared so many important papers on various aspects of Linnaeus's life and work, but also by the care taken to promote and carry out the renovation and preservation of Linnaeus's homes at Råshult, Uppsala and Hammarby, Svenska Linné-Sällskapet has earned the sincere thanks of all true naturalists.

It is hoped that our Societies may soon again enjoy the former close association that existed between us. In the meantime, it is our Society's intention to transmit to Sweden an extensive photographic record of the Linnaean Collections, which is now nearing completion.

The thanks of the Society were recorded for gifts made since the last meeting :—From Dr. W. E. Collinge, Mr. C. H. Hooper and the Queen Victoria Museum, Launceston, Tasmania.

A recommendation for election to Fellowship was read,—for the second time, in favour of Peter John Bell.

The following candidates were balloted for and elected Fellows :—Elizabeth Alice Flint, Ernest St. John Burton and John Humphrey Bell.

The President drew attention to the Sectional Committees that were being formed as an integral part of the Society's activities, and invited Fellows to take part in these meetings.

The following communication was read,—

Mrs. AGNES ARBER, D.Sc., F.L.S., Nehemiah Grew : a correction.

In a paper last year on 'Nehemiah Grew and Marcello Malpighi' (Proc. Linn. Soc., Session 153, pp. 218-38), I drew attention to a monument to Mary Grew in Christ Church, Newgate Street, and pointed out that she must have been Nehemiah Grew's first wife, but that this marriage did not appear to have been recorded previously, the 'Dictionary of National Biography' referring to one marriage only, which was, in fact, his second. Mrs. Arundell Esdaile has since drawn my attention to an article of hers in 'The Walpole Society' (xv, pp. 21-45 : 1927) dealing with John Bushnell, in which she notes the existence of Grew's first marriage, describes his first wife's monument, which she attributes to this sculptor, and gives an admirable reproduction of it, with the surmounting bust (pl. xii, c). Mrs. Esdaile suggests that it was perhaps his acquaintance with Samuel Pepys which led Grew to offer the commission to Bushnell, for this artist had already executed a similar memorial to Mrs. Pepys. This monument is reproduced in Mrs. Esdaile's memoir, side by side with that of Mary Grew ; the bust of Elizabeth Pepys shows that Bushnell had a strong feeling for facial character, so it seems likely that Mary Grew's more regular features are realistic and not merely conventional. It is to be hoped that, after the war, the broken bust may be restored and returned to its place above the tablet.

Dr. M. A. H. TINCKER, D.Sc., F.L.S., read his paper, Recent Work on Germination. (Printed in full below.)

This physiological paper was followed by a discussion, in which Mr. T. HAY, C.V.O., V.M.H., spoke on difficulties which may be encountered in germinating seeds. He was followed by Mr. G. W. ROBINSON on various factors in germinating seeds ; by Dr. J. RAMSBOTTOM, on germinating some seeds from old collections in the Department of Botany, British Museum ; and Mr. C. P. RAFFILL on some difficult seeds to import and germinate. Dr. Tincker replied to some of the points raised in the discussion.

## RECENT WORK ON GERMINATION.

By M. A. H. TINCKER, M.A., D.Sc., F.L.S.  
(Royal Horticultural Society, Wisley).

*Longevity and storage conditions.*—Crocker (1938) accepts Ewart's classification of seeds into microbiotic, living for a period not exceeding three years; mesobiotic, 3-15 years; and megabiotic, 15-100 years. Whilst both genetic and environment factors govern longevity, environment can be manipulated, and if thereby conditions that are above the average are provided for seed-storage, the seeds of many species and varieties may have their viability prolonged so that they enter a higher class. Thus, many farm and garden seeds which do not normally survive for more than 15 years can have their dormant life prolonged for many more years, the improved conditions being effected by drying, by sealed storage, by the control of temperature and of gaseous exchange. Crocker cites the ninefold prolongation of the life of *Delphinium* seeds as an example.

A report has been published by Darlington (1941) on the experiment Dr. Beale commenced in Michigan in 1879. In this experiment bottles containing seeds of common American weeds were buried in the soil at 18 inches depth for sampling periodically. After 60 years the seeds of only four plants germinated, being *Oenothera biennis*, *Silene noctiflora*, *Verbascum Blattaria*, and *Rumex crispus*.

By way of contrast to these megabiotic seeds, seeds of species of *Populus* quickly lose their capacity for germination; the Aspen (*P. tremula*) deteriorated in Moss's tests from 100 to 45 per cent. total germination in the second month of storage; *P. balsamifera* behaved similarly, but *P. Petrowskyana* lived somewhat longer and when stored at  $-5^{\circ}\text{C}$ . in a dry atmosphere 70 per cent. of the seed germinated after two years (Moss, 1938).

The effect of high moisture conditions during storage at  $70^{\circ}\text{F}$ . ( $21^{\circ}\text{C}$ .) is particularly well shown by wheat, barley and oats, as the data of Robertson, Lute and Gardner (1936) illustrate clearly. Stored under dry conditions the seed germinated well—80 per cent. after 15 years; but at high humidity the percentage was low after one year. Onion seeds may quickly deteriorate; but Beattie and Boswell (1938) found that when sealed at  $20^{\circ}\text{F}$ . ( $-7^{\circ}\text{C}$ .) they did not deteriorate in seven years. The statistical analysis of their data revealed marked interactions between moisture and temperature; for example, seeds containing 10 per cent. water deteriorated at  $40^{\circ}\text{F}$ . ( $5^{\circ}\text{C}$ .), but not so seriously at  $20^{\circ}\text{F}$ . and with only 6 or 8 per cent. moisture the deterioration was less. In a later paper the same authors (1939) recommended storage at  $34-36^{\circ}\text{F}$ . in waterproof bags; and that the seeds should contain only 6 per cent. moisture on dry weight. They emphasize the importance of correct storage particularly in oceanic regions of high humidity and temperature; and the observations of Rodrigo and Tecson (1940) made in the Philippine Islands confirm their findings; for seeds stored in air-tight containers lasted twice or three times as long as seeds in corked vessels. Barton (1935 and 1939) has published several papers dealing



with the storage of vegetable seeds, including carrot, cauliflower, lettuce, onion, tomato and egg-plant (capsicum), of which carrot, onion, tomato and capsicum benefited by dry storage which reduced the moisture content of the seed to 6 or 8 per cent. Low temperature favours longevity, and  $-5^{\circ}\text{C}$ . was found a useful storage temperature : with low relative humidity the temperature may be permitted to rise with more safety than with high humidity. In a later report, Barton (1941) reported the behaviour of lettuce, onion, tomato, flax, peanut and pine seeds stored at four different temperatures and three relative humidities. Samples starting with only 85 per cent. germination deteriorated more rapidly than others with 90 or 94 per cent. ; but the keeping qualities in the long run depended more on the storage conditions than the initial vitality. There was no precise relationship between the water taken up by a sample of seeds at a given temperature and humidity, and its percentage germination ; but certain seeds, e.g., onion, had a high, others, e.g., peanut, a low water capacity. Flower seeds in storage gave generally similar results (Barton, 1939).

Boswell and his co-workers (1940) made a further study of rapid deterioration of vegetable seeds, testing lima beans, kidney beans, maize or sweet corn, peanuts, beet, spinach, cabbage, carrots, onions and tomato. They made tests from  $80^{\circ}\text{F}$ . to  $50^{\circ}\text{F}$ . ( $27^{\circ}\text{C}$ . to  $10^{\circ}\text{C}$ .), and at approximately 45, 50, 65, 78 and 81 per cent. relative humidity ; their results were statistically analysed. With spinach, carrot, tomato and other seeds a significant tendency was observed for the seeds to contain more moisture at  $50^{\circ}\text{F}$ . than at  $80^{\circ}\text{F}$ . Within a short period of 110 days at high temperature and high humidity the germination of onion seeds fell to zero, of spinach to only 25 per cent. ; but beet and tomato maintained 70 per cent. ; after 250 days beet fell to 9 per cent., tomato maintained 70 per cent., all the others were virtually valueless at 1 per cent. or less. With low humidity and low temperature only kidney bean and sweet corn deteriorated seriously in 250 days. Samples of other seeds kept at  $32^{\circ}\text{F}$ ., and 60 per cent. humidity showed little or no deterioration ; the larger seeds were rapidly injured if warmed to  $120^{\circ}\text{F}$ . ( $49^{\circ}\text{C}$ .) or  $150^{\circ}\text{F}$ . ( $66^{\circ}\text{C}$ .). Onion seeds displayed a marked deterioration under moist conditions in six or eight months ; cabbage and carrots and spinach seed deteriorated if previously subjected to high humidity and temperature ; but beet and tomato kept relatively well.

E. H. and V. K. Toole (1939), tested at constant and at alternating temperatures the behaviour of freshly harvested seeds of species of *Brassica*, using forms of *B. campestris*, *B. juncea*, and *B. nigra* from various countries. They found that freshly harvested seed of related forms had very different requirements for germination, but as the seeds aged the speed of germination increased and the range of conditions for germination widened. These seeds showed a need for a short period of after-ripening.

Mulberry seeds also (tested by Takagi, 1939) are sensitive to humidity during storage : with a moisture-content of 7-10 per cent., 90 per cent. germinated after one year, but when kept dry with a low moisture content of 4.1 per cent., 90 per cent. germinated after seven years, and seeds were viable after 14 years if stored over calcium chloride or 44 per cent. sulphuric acid, so that the humidity was reduced to about 48 per cent.

Nelson (1940) successfully stored pine seeds (*P. laeustris*, *P. caribaea*, *P. echinata* and *P. Taeda*) in air-tight jars for seven years at temperatures of 35–38° F., whereas at room temperature they deteriorated in four years. Nelson found that stratification for 40 days in moist peatmoss favoured the germination of the loblolly and short leaf pines.

In contrast to seeds of cereals and vegetables those of *Typha Muelleri* keep well in water in jars with muslin covers, but stored dry the germination deteriorates; thus after a 19 days' test at an alternating temperature of 15° C.–29° C. in light, 95 per cent. of seed which had been kept in water for five months germinated as against only 18 per cent. of seed stored dry; in darkness the germination was lower, 40 per cent. of the seed stored in water but only 13 per cent. of that stored dry. Priester (1941) considers that the spread of this reed in the water-channels of New South Wales cannot be readily prevented.

For many years lettuce seed has been known to be troublesome in its germination; cultivated varieties differ in this respect, and individual plants may produce seed differing from that of neighbouring plants. Thompson (1937) states that races such as 'Iceberg' which produces seed only sparsely, gives less dormant seed than 'Grand Rapids,' a heavy seeder. Fertilisers added to the soil greatly increased the percentage germination of the seed subsequently produced. In American commercial practice several harvests of seed are made; whilst the first harvest produces larger seed than later harvests, the later seed may germinate better. Thus the stage of development of the parent plant also influences dormancy and germination. Thompson (1938) failed to find an optimum combination for germination of the factors light, temperature, aeration and moisture; and found no factor alone critical. A low temperature fluctuating around 5°–10° C. followed during the germination test by a rise in temperature to 20°–25° C. proved effective in increasing the percentage germination. Shuck (1934 and 1935) found in tests at 25° C. or 30° C. that light could overcome the tendency for freshly harvested seed to remain dormant. Low temperature and moisture broke the dormancy if light was available. Barton (1939) also obtained satisfactory germination by a chilling treatment of moist seed at 1° C. or 5° C. for several (1–7) days without which few seeds germinated. The chilled seed could be dried and stored for a few days without losing the capacity for rapid germination. Possibly the hydrolysis of fats known to commence quickly (Griffiths, 1938) may be started by the moistening of the seed.

With other varieties of lettuce Wharton and Frazier (1938) noticed that freshly harvested seed failed to germinate, but that seed stored for two years at 40° F., with 50 per cent. relative humidity germinated well. Storage conditions of new seed had a pronounced effect on germination, for 95 per cent. of seed harvested in May germinated well in August after storage at 75°–80° F., with 50 per cent. humidity; but of seed stored at only 10° F. with 75 per cent. humidity the germination was very poor. Later Frazier (1939) reported from Arizona that early harvested large seeds gave more vigorous seedlings when grown under the high temperature conditions of the Arizona early autumn. A temperature as high as 130° F. during storage was not as advantageous as 75°–88° F.

Odland (1937), working with seeds of Cucurbitaceae found that those of cucumbers, pumpkins, musk and water melons required for satisfactory germination a period of several weeks after-ripening; the germination of new pumpkin seed rising from 36 per cent. to 62 per cent. in 20 weeks. Other cucurbitaceous seeds require a longer period for after-ripening. As Choate (1940) has shown with *Echinocystis lobata* one or two years old seed germinates well: its freshly harvested seed when stored at 5° C. for 20-26 weeks will also germinate. Tomato and capsicum seed did not require this storage period.

*Hard seeds.*—The prevention of absorption of water by hard seed coats is a well-known cause of dormancy. Recently further examples have been studied, the Sea pea, *Lathyrus maritimus*, develops a hard coat some weeks after harvest. Dinnis and Jordan (1941) have studied the effect of strong sulphuric acid on the seed coat and on germination; they recommend a period of quarter- or half-hour treatment finding it to cause 94 per cent. and 70 per cent. germination as against 17 per cent. without acid treatment. Small immature seed gathered before the coat had become hard did not germinate; but well-developed seeds obtained when the testa was quite moist and readily removable without injury to the embryo germinated fairly satisfactorily to the extent of 75 per cent.

Richaria and Dhodapkar (1940) reported the occurrence of hard seed in Indian samples of sesame (*Sesamum indicum*). No low temperatures employed by Dunn (1939) improved the seed of Sweet Clover (*Melilotus* sp.) and Smooth Vetch (*Vicia tetrasperma*) more than room temperature, whereas temperatures during storage which alternated proved harmful and did not hasten germination of the hard seeds produced by these plants.

Various methods of breaking or weakening the hard seed coats have been practised; with the larger seeds filing is possible, and success has been obtained at Wisley in germinating seeds of *Abrus*, *Cassia*, *Adenanthera* and *Pithecellobium*, etc. Dahle (1938) states that the germination of seed of *Hevea* can be hastened by filing with a saw, an operation which is possible at the rate of 200 an hour.

The germination and emergence of the seedlings from stony endocarps have been figured and described by Hill (1937).

*After-ripening and stratification.*—The extensive series of investigations on Coniferous, Rosaceous and other seeds by numerous workers at the Boyce Thompson Institute in recent years has been reviewed by Barton (1939). She lists almost a hundred plants whose seeds benefit by moist storage at a cool temperature of between 33° F. and 49° F., for periods varying from one to five months. The majority of these require only two or three months chilling before sowing at higher temperatures. The 'seeds' or achenes may be kept moist in sand, moss, peat, sphagnum or other material. The after-ripening process is no doubt associated with biochemical changes that the reserve fats and oils undergo; naturally this takes place in the winter when, in temperate regions, the soil surface-layers vary within the above-named temperatures for prolonged periods. The successful germination of the Mazzard cherry by such treatment affords a striking illustration: after cold treatment almost every seed grew quickly; whilst without such treatment immediate germination was nil. The oily seeds of many pines have responded favourably.



Using sand as a stratification medium tests were made at Wisley with some twenty species of roses (Tincker, 1935). Stratification around 5° C. gave better germination than cold storage between - 2° C. and 2° C., whether moist or dry. A charring of the thick coats of the achenes for three hours with concentrated sulphuric acid causes a slight acceleration of germination in some species. In the genus *Cotoneaster* the percentage of fruits containing well-formed achenes was often low. The number of established seedlings of roses or cotoneasters obtained within a year was never very high; but without the chilling pre-treatment germination was very slow.

Since that work was carried out the investigations of the Boyce Thompson Institute have shown that in *Cotoneaster* and some other genera two distinct pre-treatments may be necessary, one of higher temperature, 77° F., for three months, followed by the lower chilling storage for perhaps three to six months. During the former, the hard coat decays, probably aided by bacterial or fungal action; during the cool period after-ripening proceeds. Amongst responsive 'seeds' may be mentioned those of *Cotoneaster horizontalis*, *Crataegus Oxyantha* and *Taxus cuspidata*. Such treatments resemble the conditions under which seeds sown in late spring in the open ground in temperate regions germinate in the following early spring; but seeds falling to the ground in autumn might not germinate for 18 months. To ensure germination it is necessary both to weaken the hard coat and to bring about the adequate after-ripening of the embryo. Such methods have given success with *Tilia*, *Symphoricarpos*, *Crataegus*, *Halesia carolina*, *Cotoneaster* sp. and *Arctostaphylos Uva-ursi* in addition to the above-mentioned species.

The Boyce Thompson work does not lack ample confirmation, of which a few examples must suffice. With *Rubus* and *Ribes* the removal of the seed from the fruit followed by stratification, in leaf-mould preferably, induced successful germination, but dry storage was a failure in Furtauer's tests (1941). With pear seeds Zelensky (1939) found that a period of 57 days' stratification gave 85 per cent. germination, whereas 37 days was too short a time, causing only 5 per cent. germination. *Pyrus elaeagnifolium* gave somewhat similar results. With peach seeds Scott and Waugh (1940) tested sand, quartz, peat and humus, and also vitamin B<sub>1</sub>, and indolylbutyric acid as materials likely to influence subsequent germination. The after-ripening processes required at least 65 days; 115 days at 40° F. with 85 to 95 per cent. relative humidity, proved an effective treatment. When the embryo was removed from the hard endocarp the germination after 65 days' treatment was as good as after 115 days.

Other seeds mature in dry storage, examples of which have already been mentioned, such as the Brassicas and Cucurbitaceae, but a recently studied case is *Impatiens Balsamina*, which requires from four to six months at 25° C.; pre-treatment of fresh seeds at 5° C., moist, proved favourable, but such chilling had, however, no effect on seed already after-ripened. Somewhat similar responses had been observed previously by Simpson (1935) with cotton and *Nicotiana rustica*, which require about three to five months' dry storage. Burkill (1939) states that *Tanais communis* requires six months' moist storage followed by low temperatures



for germination. If the low temperatures do not occur a new period of dormancy ensues.

*Epicotyl Dormancy.*—Seeds of certain plants, including lilies, may germinate as far as the production of a rootlet, but no signs of a shoot appear for a considerable time—often for a further year. Taylor (1932) emphasizes the value of autumn sowing for *L. auratum*, *L. canadense*, *L. croceum*, *L. dalmaticum*, *L. monadelphum*, *L. pardalinum*, etc.; for other species he preferred spring sowing. Stern (1933), confirming Stout's classification, grouped lilies into classes according to the behaviour of the seedlings, (i) those in which a green cotyledon develops above ground such as *L. formosanum*, *L. Martagon*, *L. regale* and *L. Willmottiae* (ii) others with underground germination, the cotyledon being embedded in the seed, such as *L. japonicum* and *L. columbianum*, and in these the shoot develops a year after germination, and (iii) others in which a very small bulb first forms and from which during the second year a leaf develops, he cites *L. monadelphum*, *L. canadense* and *L. distichum* as examples. Barton's results (1936) of experiments made with lilies at different temperatures assist in explanation. The seeds of *L. auratum*, *L. canadense*, *L. japonicum*, *L. rubellum*, *L. superbum* and *L. Szovitsianum* required a period of three to six months at about 20° C. for root growth: they then need a shorter period of six to twelve weeks at a low temperature, 1°–10° C., to start the growth of the first leaves. Using greenhouses and cool rooms, Barton caused seedlings to appear above ground in a year. Thus in practice spring and summer planting in the open is advantageous but late autumn and winter sowing offers no advantage.

As opportunity has occurred, tests have been made with many kinds of lily seeds at Wisley. With *L. auratum* moist storage at 6° C. for one month greatly accelerated the growth of the epicotyls. With *L. maritimum*, *L. parvum*, *L. pardalinum*, *L. occidentale* sown in late spring, transference of the boxes to the cold conditions of winter has resulted in successful germination (over 75 per cent.) in the subsequent spring, whereas in similar boxes kept during the winter in a warm greenhouse the resulting above-surface germination was poor (below 15 per cent.). *L. rubellum* has given somewhat similar results. How long the growth of the epicotyl may be delayed appears uncertain, but two years elapsed before the appearance of shoots of *L. rubellum*, when the boxes in which the seeds had been sown were kept warm in a greenhouse. In *L. columbianum*, *L. Humboldtii* (two varieties), *L. Kelloggi*, *L. maritimum*, *L. occidentale*, *L. pardalinum*, *L. Washingtonianum* 'underground' germination was readily obtained, but there was a long delay of six to eight months before any growth was visible above the surface. Dressing the seed with zinc oxide failed to influence either aspect of germination with these species or with *L. formosanum* which germinates rapidly. Proprietary powders containing mercury compounds used as seed dressings were without effect on the germination of *L. formosanum*, *L. regale*, *L. pardalinum*, *L. giganteum*, *L. Martagon* and *L. pomponium*. Seed soaking for four days at 20° C., 10° C. and 1° C. was generally ineffective; but, as stated above, moist storage around 5° C. for a month proved effective in hastening epicotyl growth.

*Alternating temperatures: Grasses.*—Alternating temperatures, in

periods usually of 18 hours at the lower and six at the higher range, favour germination of many grass seeds. The range varies with species. With *Panicum obtusum* 20° C. and 35° C. proved best; with *Setaria macrostachya* 10° C. and 35° C. (V. K. Toole, 1940); with *Digitaria Ischaemum* a period of eight weeks pre-chilling at 3° C. proved effective in hastening germination, and 20° C./40° C. proved a useful temperature combination for germination: *D. sanguinalis* responded to one month's chilling, moist, at 3° C. and germinated at 20° C., 35° C. The seed of *D. Ischaemum* responded favourably to the addition of a trace of nitrates (0.2 per cent. potassium nitrate) at 15° C./25° C. or 20° C./30° C., but at 20° C./35° C. and 20° C./40° C. this had a retarding effect. Nitrates were not effective with *D. sanguinalis*: light had no effect on *D. Ischaemum*, but decreased the rate of germination with *D. sanguinalis* (V. K. Toole, 1941). Working with *Sporobolus cryptandrus*, the seed proved resistant to alternating temperatures and nitrates, but responded to a short two-minute exposure to 71 per cent. sulphuric acid. Other species, *S. flexuosus* and *S. giganteus*, gave poor percentages in a wide range of tests, but also responded favourably to 71 per cent. sulphuric acid.

**Light.**—It is well known that light, and its absence, influences germination. The seeds of many Gesneraceae, of *Lythrum salicaria* (strains of which are particularly sensitive), *Nicotiana Tabacum* and *Mimulus ringens* (Hutchings, 1936), etc., germinate better in the light; the seeds of *Nemophila insignia*, *Nigella damascena* and *Phacelia tanacetifolia*, etc., germinate better in darkness. With *Mimulus* this is not a seed-coat effect. Recently it has been found that seeds of *Striga densiflora* germinate better in darkness, but that seeds of *S. euphrasioides* germinate better in light; but that the effect is reversed if tested in the presence of the host plant (Kumara, 1940).

A further analysis of the influence of light on seeds shows that certain bands of the spectrum are responsible. Aneli (1940) reports the inhibiting action of blue light on the germination of tomato. Resuhr (1939) reported that red light of 700–750  $\mu\mu$ , blue of 475–490  $\mu\mu$ , and violet of 450  $\mu\mu$  inhibited the germination of 'dark-germinating' *Amaranthus*, but orange red of 675  $\mu\mu$  stimulated germination. With *Phacelia* inhibition occurred in the spectrum at 350  $\mu\mu$  to 450  $\mu\mu$  (violet) and more strongly at 640  $\mu\mu$  (orange). In both cases the effect was on the seed-coats, for when they were broken germination occurred in otherwise unfavourable light.

With lettuce seed Shuck (1935) found that short wave-lengths of light were more effective than daylight in producing dormancy in seed moistened by placing it in a humid atmosphere, and again dried in light, followed by germination-tests made in darkness at 20° C. If dried in darkness the percentage germination was very high, almost 100 per cent. Flint (1934) found that light of long wave-lengths promoted germination, that of short wave-lengths retarded it.

Masumoto (1939), experimenting on tobacco seed which had not undergone a period of after-ripening, observed that warming at 30° C. to 70° C. favoured germination and displaced the need for light; but that at 80° C. deleterious effects reduced the vitality of the seed. Heating fully after-ripened seed to 70° C. also was disadvantageous.

An interesting article in 'The Gardeners' Chronicle', 1941, reports experiments made by a business seed-house in Copenhagen in which quartz and sollux lamps were used to illuminate dry seeds for one hour. The subsequent germination after long storage was reported to be materially improved, e.g., cauliflower seed of 1932, tested in 1940, gave 50 per cent., but treated seed of 1933 tested against it gave 85 per cent., and parsnips, well known to give low percentages, benefited similarly. Seed of 1937 tested in 1940 gave 50 per cent. and treated seed of 1937 tested against it gave 80 per cent. Seeds of onions and leeks, treated immediately after harvesting retained their germination capacity longer. Confirmation of these observations is needed, and full details of the treatments have not yet become available.

However, there can be no doubt that many more seeds will be shown to be sensitive to light than these. Tests made at Wisley with a few species of *Primula* (Tincker, 1935) showed that *P. Littoniana*, tested in January, being one year old, germinated 82 per cent. in light, but only 20 per cent. in darkness, at 19° C., and at fluctuating temperatures 16° C./18° C. in light 90 per cent., in darkness 1 per cent. *P. Florindae* was slightly sensitive, others such as *P. microdonta*, *P. alpicola*, *P. violacea*, *P. Winteri* and *P. magellanica* gave negative results. The seeds of this genus are frequently troublesome, and further physiological study would be repaid.

*Oxygen*.—It has long been realized that an inadequate supply of oxygen may prolong dormancy and the critical oxygen requirements of *Xanthium* and other seeds have been determined; but more recently attention has been focused on seeds that require very little oxygen for germination: e.g., rice. Other water plants whose seeds need little oxygen are *Alisma plantago*, *Nelumbium Nelumbo*, whose longevity is remarkable, *Trapa natans* and *Typha latifolia*. Working with *Typha* Moringa (1926) obtained 96 per cent. germination in an atmosphere of 40–80 per cent. hydrogen or nitrogen whilst 20 per cent. oxygen depressed germination almost to 1 per cent. Quite a number of seeds have been found to germinate satisfactorily under water with a very limited supply of oxygen; of 78 genera from 24 families, 43 species gave good germination in water.

Stier (1937) found that low temperature storage of moist seeds of potato did not result in satisfactory germination, neither did high temperature drying at 72° C. Treatments with alcohol, hydrogen peroxide or sulphuric acid proved generally ineffective, but excision of the radicle and removal of the testa and part of the endosperm significantly accelerated germination. Stier considered that the free entry of oxygen to the embryo was prevented by the thick outer walls of the nucellar layer until, presumably later, a change came permitting ready germination. A similar explanation has been put forward by Spaeth (1934) to account for the dormancy of *Tilia* seed.

Direct measurements of the permeability to gases of the seed membranes have been made by R. Brown (1940) working with *Cucurbita Pepo*. He found the inner seed-coat membrane the controlling factor in gaseous exchange, a membrane of five layers, built up from the nucellus and endo-



sperm. Complete saturation by water of the membrane rendered it less permeable than when dry: the impermeability was associated with a living layer of cells; chloroform-treatment increased permeability.

The acorns of *Quercus alba* germinate freely in October and November, those of *Q. borealis* (the Northern Red Oak) require a period of after-ripening: and storage temperatures largely govern subsequent behaviour. Stored moist between 0° C. and 10° C. until spring, a germination of 80 or 90 per cent. occurs in three weeks in spring, stored at 20° C. only 5 per cent. or so grow. J. Brown (1939) studied the respiration of these acorns at controlled temperatures, and was not able to find any major points of difference. It is stated that the Northern Oak contains more fats, and that in both species during winter storage the fat decreases as carbohydrates accumulate. The low respiratory quotients found by Brown support these statements, but it is surprising that there was not a greater difference in respiratory activity between the two species. The amount of oxygen consumed by both species rose after three weeks' storage. The one point of difference was that the respiratory quotient of *Q. borealis* decreased more rapidly at low temperatures, suggesting that carbohydrate accumulation began earlier and proceeded faster. The production of carbon dioxide was more constant than the oxygen consumed and was less affected, presumably, by chemical transformations of the reserve food substances; it did not give such a good indication of the chemical changes of the food substances involved during after-ripening. Yet despite these considerations the main feature was the similarity in respiration of the two species, not their difference.

*Size and Maturity of Embryo.*—The embryos in the achenes of the Ash (*Fraxinus excelsior*) may be dormant for several years in soil; the embryo, which extends little more than half the length of the seed, removed from the fruit requires time to develop in size: stratification is not immediately effective. But in *F. americana*, *F. pennsylvanica* and its variety *lanceolata* according to Steinbauer (1937) the embryo extends to the full length of the seed, and after one or two months' stratification at 5° C. germination takes place. The black ash, *F. nigra*, more closely resembles the European ash, *F. excelsior*, in size of embryo, which is short; and it also requires time for the growth in length and size of the embryo. At 5° C. during stratification the formation of starch and soluble carbohydrates is accelerated as compared with high temperature storage, but the embryos grow faster in the black ash at higher temperatures, 20° C. and 30° C., and reach their maximum length quickly. Little growth takes place at 5° C.

Immature embryos removed from the fruits and grown in artificial culture may show unusual growth patterns producing curiously abnormal seedlings as in the case of the apple, pear, peach, cherry, plum and apricot. These dwarfs do not pass through the normal growth stages, but after some time, 30 days or so, may commence more normal development. Tukey (1938) has provided illustrations of such seedlings. A critical quantitative study of the growth substances and their distribution in the tissue during this period would probably give some highly informative data.

The question of large and small seed arises again, Kusmitscheiva (1939) claims that larger seeds of several vegetables, particularly radish, grew



quicker and the subsequent plants ripened earlier than those from smaller seed. Larger seeds of *Cucurbita* gave better germination than smaller seed. But taking an extreme case Nutman (1941) found the dwarf embryos of rye viable five days after fertilization, when the grain was only one-sixteenth of the normal grain weight; yet their relative growth-rate exceeded the normal rate so much that the plants derived from such minute embryos attained in approximately five months the same size as that reached by plants from much heavier seed.

*Examples of Chemical Stimulation and Inhibition.*—The influence of a number of chemical substances on dormant lettuce seed was studied by Thompson and Kosar (1939), who found sulphur compounds effective in causing germination and particularly so if the sulphur occurred as a thiocyanide. Thiourea and potassium thiocyanide proved useful stimulants.

Luck (1941), working with species of *Pyrola*, states that the earlier phases of germination are frequently followed by a second period of relative inactivity. When vitamins, yeast extracts, or fungi failed to stimulate germination, soil extracts met with some success, but the responsible compounds remain as yet to be isolated, identified and their use fully investigated.

With sugar beet the fruit has been shown by Tolman and Stedt (1940) to contain a water-soluble substance which has a toxic effect on germination. It can be removed by washing for six hours, when the subsequent percentage germination is increased. Further details of its nature are now available, and ammonia is probably the toxic substance.

Small traces of ethylene in the air, one part per thousand for three days, increased the rate of maturation of stored wheat. The grain quickly attained the milling state, and some increase in viability was also reported by Ballsak and Hale (1940). Ethylene chlorhydrin has been mentioned as a substance to break seed dormancy, but detailed reports are not available.

The deleterious effect of soaking dwarf bean seed has long been known, but recently Eyster (1940) studied the solutes removed in the process which include proteins, enzymes and growth substances, all of whose loss was inversely proportional to subsequent germination.

*Growth substances.*—The successful initiation of roots from cuttings to which growth substances such as indolyl butyric, indolyl acetic, or naphthalene acetic acid was applied aroused interest in the possibility of stimulating the development of the radicle of seeds. Davies, Atkins and Hudson (1936 and 1937) using oats, mustard and cress, reported that such compounds retarded germination. Russian workers (Cajlachjan and Zdanova, 1938) obtained similar results with wheat, oats, millet, vetch, hemp, flax and peas. With further non-dormant seeds Barton (1938) confirmed these observations on onions, tomato, radish, beet and turnip, with dormant seeds including *Cornus florida*, *C. stolonifera*, and apple, no immediate germination resulted. Youden (1940) observed no stimulation with Soy beans; in these tests the growth substances were applied mixed with talc. With the grasses, *Agrostis tenuis* and *Poa pratensis*, Defrance (1941) also obtained negative results; and with about thirty-six

perennials Chadwick and Swartley (1941) found that seed treatments were ineffective. With Delphiniums, seven species of lilies and with peas the use of solutions and dusts containing active growth substances failed to accelerate germination in Wisley tests (Tincker, 1940). Croxall and Ogilvie (1941) report that seed dressings containing growth substances did not increase the yield of lettuce, tomato, sugar beet or dwarf beans when applied with talc as a carrier. Minnum (1941) also failed to obtain positive results with various vegetables. Thus there is a considerable weight of evidence indicating that growth substances have not been successfully applied to seeds to solve germination problems despite some of the earlier favourable claims.

*Fungal Invasion.*—It is not here possible to review adequately the mycorrhizal problems of symbiosis, but it has been shown by Gordon (1937) that the endophytic fungus in the roots of *Rhododendrons* such as *R. decorum*, *R. ambiguum* is not necessary for the early stages of germination, and the mycelium is not seed-borne as in *Erica*. The deleterious effect of fungal invasion of the seed upon subsequent germination is well shown from the studies of Toole and his co-workers (1940) in the case of the Egg plant infected by *Phomopsis vexans*, the mycelium of which is seed-borne.

*Soil and High Temperatures.*—The effect of soil temperature on the germination of Citrus seeds has been studied in Florida by Camp and his co-workers (1933). Whilst no precise maximum, minimum, or optimum soil temperature was exactly ascertainable, the optimum lay between 31° C. and 35° C., the lower limit about 15° C. and the maximum below 40° C. The lemon and the sour orange had a higher optimum temperature than the grape-fruit and the sweet orange. These may appear to be high figures for soil temperatures, but they are low compared with the soil temperatures that certain Australian woody seeds will withstand, as Beadle (1940) has shown, e.g., *Hakea acicularis*, *Casuarina rigida*, *Leptospermum scoparium*, *Banksia serrata* and *Acacia decurrens*, which can resist 110° C. for four hours and whose remarkable germination after forest fires has long been known. Beadle considered that many woody fruits dehisce after charring. He recorded the soil temperatures at various depths under fires of approximately one hour, two hours and eight hours duration, at 3 inches; for example the maxima attained were 59° C., 95° C., and 230° C., but at 6 inches only 35° C., 60° C., and 81° C., so that woody seed at that depth had a good chance of survival. The ligneous tubers of Proteaceous and Myrtaceous plants were also partially 'fire-proof'.

In India, Parija and Mallik (1940) compared the resistance of oily with starchy seeds and found that oily seeds of *Brassica campestris*, *Sesamum indicum* and *Helianthus annuus* resisted high temperature better than starchy seeds, the greater the oil content the more resistant the seeds to temperature ranging between 40° C. and 60° C. for periods of from 8 to 120 hours.

*Miscellaneous.*—From Java interesting reports have come (Zweede, 1940, and Eikema, 1941) of valuable seeds of high yielding strains of

*Herea* being split by Dutch growers into two segments at an early stage of germination. The dividing cut was made before the emergence of the cotyledons from the seed, when radicle and plumule were out, but the whole seedling yet held by the seed coat. In Gambard's method, possibly the most successful, the stronger seedlings were cut longitudinally above the junction of plumule and cotyledons, leaving on one segment the plumule intact, one cotyledon and half the radicle, the other segment consisted of one cotyledon and half the radicle; the development of the bud in the axil of the cotyledon proceeded so well that this 'twin' did not lag in development far behind the other. Moist conditions were provided by using powdered charcoal holding 40 per cent. water and by shading. Paraffined paper was used to separate the root systems to facilitate later handling for transference. In Ramaer's method, also satisfactory, the cut involved division of the plumule: but cutting twice to make triplet seedlings proved unsatisfactory, for too high a proportion of the side segments died.

*Seed germination and lunar phases.*—In a series of tests made at the John Innes Horticultural Institution with vegetable seeds, Mather and Newell (1941) failed to detect that sowing in the garden at any of the four quarters of the moon influenced the time taken for germination. Under glass the rate of germination of the seeds was more nearly constant, and despite some irregularities not fully explicable, in one month's sowings there was no reliable evidence forthcoming that the phase of the moon at which sowing took place consistently influenced germination.

Whinnett (1941) recently reported earlier experiments, and also failed to detect any lunar effect with vegetable seeds during their germination.

*Rapid methods of determining viability.*—From time to time various biochemical tests, such as the catalase reaction, have been put forward as rapid methods of testing for viability. More recently the widespread success attained in growing excised embryos artificially has favoured this as a method of rapid testing; and close agreement has been obtained between the behaviour of embryos removed and tested, and germination tests made with after-ripened seed.

*Cytology and dormancy.*—The differences in cytological details between dormant cells and active ones have been studied by Middendorf (1939), who found in *Phaseolus* and *Tea* that the dormant cell was "plasmolyzed" and possessed a nucleus of irregular shape lacking a defined membrane, and the nucleolus was not optically differentiated, the vacuoles were small and the mitochondria appeared as small granules or spheres. On germination the cells were turgid, the well-defined nucleus spherical, the nucleolus optically differentiated, and the protoplasm contained vacuoles and with rod-like or filament mitochondria.

*Seed Treatments and aftergrowth.*—The fascinating chapter of physiology concerned with seed treatments and subsequent growth, including vernalization (yarovization) and similar phenomena, falls outside the scope of the present article. How far the claims of Russian workers will be confirmed in field trials in this country we cannot yet state; but



the work carried out with rye by Purvis (1934) and with tomatoes where the early crop was increased, as reported by Goodall and Bolas (1942), affords much promise.

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Mr. T. HAY referred to the way in which seeds of the Hydrophyllaceae *Emmenanthe penduliflora* and the Papaveraceae *Romneya Coulteri* germinate if sown in soil that has been heated and to the curious difference which results from the position in which the seeds of *Grevillea robusta* lie, these germinating better if edge upwards than if flat. The seeds of the Scrophulariaceae *Nemesia strumosa*, a native of S. Africa, start into life at a much lower temperature than would be expected from its origin. He commented on the frequency of two-year old seed being better than new seed, and finally narrated how *Lathyrus magellanicus* has been reintroduced to Britain.

#### Mr. G. W. ROBINSON :

In the routine of Botanic Gardens the raising of plants from seed is one of the most important aspects of the work. It involves, of course, the raising of species from all climates and all parts of the world, and the germination of all types of 'seed' (sensu lato) from the fine dust-like seed of the Gesneraceae to the huge Palm fruits of which the most extreme case is probably *Lodoicea seychellarum* or Coco-de-mer : and it requires two years from the commencement of germination to its complete severance from the nut, which has to be 'sown' in a tub.

Success is largely dependent on a knowledge of the habitats and conditions of the species under treatment, and they are usually dealt with under three main groups.

*Tropical plants* requiring high humidity and temperature, and usually propagating cases with bottom heat.

*Temperate plants*, which includes most 'succulents', and the great majority of Australian, New Zealand and S. African species which require cooler and more airy conditions.

*Hardy plants* embracing the great mass of trees, shrubs, hardy plants, and Alpines which require little or no artificial heat for germination.

These broad groups are to some extent split up by the individual requirements of bog plants and aquatics, some of which require considerable heat, e.g., *Victoria regia* will not germinate in a temperature below 80° F. Lime-loving and lime-hating species must be specially catered for and provision made for additional drainage in the case of succulents.

It may safely be said, however, that the vast majority of seeds only require a sweet, clean compost, efficient drainage, and reasonable care and attention to secure germination.

As is well known, there are a large number of hardy plants, seed of which should be sown at the earliest possible moment, even before fully ripe, to secure immediate germination; for example, certain *Primulas* (the *sonchifolia* and *candelabra* groups in particular), *Helleborus* and other *Ranunculaceae*. These same seeds if not sown quickly will frequently take months or even years to germinate. Regarding longevity in seeds, my own most interesting experience was the sight of thousands of *Sisyrinchium striatum* flowering where eighteen months previously had been dense evergreen woods; this was in the Valparaiso district of Chile. *Iridaceae*, to which this species belongs, are not normally regarded as having hard or macrobiotic seeds. The Foxglove frequently flowers in Britain in the same way.

In the acceleration of germination of really hard seeds the 'bush-fire' method may be used with good results by heating them on a shovel. Points in Dr. Tincker's paper which impressed me most as being of vital importance to the practical gardener are, firstly, the method he describes of forcing *Lilies* into growth by changes in temperature, for nothing is more annoying than to have pans of partially germinated seed which will not move.

Stratification is also an immense economy over the old method of immediate sowing in the saving of frame space for a whole season. The research on the effect of light on germination is again of great practical importance as his tables showed. It is my experience also that Australian and S. African plants in particular, require full exposure the moment they show signs of germination or they will fail.

Dr. J. RAMSBOTTOM described experiments which he had initiated recently, with old seeds obtained from the collections in the British Museum. One experiment was with seeds of *Albizzia Julibrissin* brought back from China by Sir George Staunton's mission in 1793. His attention had been drawn to their vitality by finding that some of them had germinated from being wetted in the operation of extinguishing a fire in the Museum in September 1940. Three of these seeds had been planted in the Chelsea Physic Garden, and though two had met with a subsequent accident, one was growing. The seed had been stored for 147 years. The second experiment was with *Nelumbium Nelumbo*. Three seedlings of this were exhibited. Two had been raised from seeds presented to the Museum by Professor I. Ogha in 1926; they had been obtained from



a prehistoric peat bed in the Pulantien Basin, Southern Manchuria, and estimated as at least 300 to 400 years. The seeds, after the removal of their seed-coats, germinated in water at 32° C., one after twenty-one hours, the other after a slightly longer period. The third seedling of *Nelumbium* had been raised from a seed taken from a receptacle in the Sloane collections. Seeds from this same collection, then at least 150 years old, had been sown by Robert Brown between 1843 and 1855 and fourteen germinations obtained. The single seed taken for Dr. Ramsbottom's experiment produced a shoot at once, which was half an inch long within twenty-one hours and more than an inch on the second day. The experiments are being continued.

Mr. C. P. RAFFILL gave an account of difficulties experienced at Kew in germinating seeds of exotic plants. Those which come from Malaya, South America, eastern Australia, east and west Africa, and Ceylon, are generally troublesome, and this often because they die when dried.

Of dying when dried *Magnolia* supplies a good illustration, seed from China and from the Himalaya giving no results if despatched quite dry, but some return if sent moist. The seeds of the related genus *Michelia* are short-lived. Like *Magnolia*, seed of *Nothofagus* dies if dried.

## PROCEEDINGS OF THE ANNIVERSARY MEETING

28 May 1942

Dr. E. S. RUSSELL, O.B.E., M.A., President,  
in the Chair.

The Proceedings of the General Meeting held on Thursday, 14 May 1942, having been circulated, were taken as read and confirmed.

The President reported the deaths of the following Fellows :—Mr. R. H. Corstorphine and Mr. W. P. Pycraft.

The following Fellows signed the Obligation in the Book of the Charter and Bye-Laws and were admitted :—Harold Cyril Bibby and Elizabeth Alice Flint.

The Financial Report was given by the Deputy Treasurer and the Accounts of the Society, duly audited, for the year 1941-42 were laid before the meeting.

On a motion by Mr. R. WINCKWORTH, seconded by Sir GEOFFREY EVANS, C.I.E., the Report and Statement of Accounts were adopted.

The Bye-Laws regulating the Election of Council and Officers having been read by the Assistant Secretary, the PRESIDENT declared the Ballot for Council and Officers to be open, and voting began. The Ballots for Council and Officers were closed at the due time.

Meanwhile the Librarian and Assistant Secretary presented his Report.

**LIST OF THE SOCIETY.**—Since the last Anniversary Meeting the Society has lost 40 members. The detailed statement is as follows,—

**18 FELLOWS BY DEATH.**—Mahbub Alam, Rose Bracher, Marian, Lady Busk, Frederick Berry-Lewis Butler, Robert Henry Corstorphine, John Guy Dollman, Robert John Flintoff, Benjamin Millard Griffiths, Arthur Grove, Patrick Martin Hall, Arthur W. Hill, K.C.M.G., John William Haigh Johnson, Arthur Francis George Kerr, Charles Arnold Newman, Charles Oldham, William Plane Pycraft, James Levi Sager, John Joseph Sheldon.

**2 FOREIGN MEMBERS BY DEATH.**—Hans Schinz, Hans Spemann.

**2 ASSOCIATES BY DEATH.**—Rev. Harry Joseph Riddelsdell, Charles Henry Wright.

**17 FELLOWS BY WITHDRAWAL.**—James Wales Audas, Wilfred Norman Edwards, Moore Betty Fullerton, Eleanor Mary Hughes Gibb, Godfrey Michael Graham, Leslie Beeching Hall, Frederick Ronald Hayes, Thomas Ashton Lofthouse, Thomas Alan Oxley, James Small, James Smith, Frank Arthur Stockdale, K.C.M.G., Ernest John Stream, Richard John Tabor, Clarence Tierney, George Fox Wilson, Marjorie Alison Wilson.

**1 REMOVAL FROM THE LIST.**—Joseph Ivan Armstrong.

During the Session 18 Fellows and 1 Associate have been elected. Of the 18 Fellows elected, 16 have qualified. The present number in the List of Fellows is 632, with 2 Fellows elected but not yet qualified.

**LIBRARY.**—Between 1 May 1941 and 30 April 1942 56 books, 278 parts of periodical publications, and 40 reprints have been presented. During the same period the number of volumes bound was 112.

The number of volumes borrowed by Fellows and Associates was 470 and by the National Central Library 108. 226 signatures were recorded in the Library Visitors' book.

**LINNAEAN COLLECTIONS.**—During the Session the task of photographing the Linnaean Collections and of checking the films has been proceeded with; and a series of films comprising in all about 40,000 photographs is now nearing completion.

At the conclusion of this report the PRESIDENT appointed Mr. D. J. SCOURFIELD, I.S.O., Dr. MARGARET A. BRETT and Mr. N. Y. SANDWITH as Scrutineers of the Ballot.

He reviewed the welfare of the Society as follows:—

This year I have a more cheerful report to give you. Our Rooms have suffered no further damage from the malice of the enemy, and our meetings have been held regularly, except for the winter break, which experience has shown to be advisable on account of the black-out. Attendances at the General Meetings have distinctly improved with the coming of longer days, and the Session will be extended, as last year, into July. While we have welcomed 18 new Fellows in the course of the year

our ranks have been somewhat depleted by deaths and withdrawals, and the roll now stands at 632. We especially mourn the death of Sir Arthur Hill, the Director of Kew, a most distinguished botanist and a good friend to the Society. Subscriptions from Fellows abroad have been in many cases difficult to collect; but this trouble, as the Deputy Treasurer has told us, is being surmounted, and a small number serving with the Armed Forces have been granted remission or reduction of their contribution under the Bye-law we passed last year.

In order to strengthen the Society, the Council has considered various suggestions for making membership more attractive to the younger biologists, but has not yet reached the stage of making definite recommendations. This will be an important task for the new Council, who should at the same time undertake a general revision of the Bye-laws. A new departure has been made by the formation of Sectional Committees. The Council felt that it would be of advantage for those interested in particular groups of animals and plants to meet and discuss their common problems and interests, and the scheme was inaugurated by the recent constitution of a Crustacea Section, under the Chairmanship of Dr. Isabella Gordon, and a Marine Algæ Section presided over by Dr. E. Marion Delf. While the Sections are definitely part of the Society's organization, they will be freely open to non-members and students, on the invitation of the Chairmen, and the collaboration of specialist societies will be welcomed. I regard this as a promising development of our activities and one likely to be of benefit to the Society.

A special feature of this Session has been the holding of discussions on subjects of general interest, such as the bio-geographical division of the Indo-Australian region, and the germination of seeds; these have been successful and well-attended meetings.

At one or two of our General Meetings we extended the hospitality of our Rooms to the Zoological Society, several of whose Fellows communicated papers of zoological interest. We have been represented at the Conference on Nature Preservation by our Secretaries, who are thus in a position to convey the views of the Society to authoritative quarters. Miss M. S. Campbell has represented the Society on the Phenological Committee of the Royal Meteorological Society.

The state of the Library has given the Council some concern. Not only are the shelves greatly overcrowded, double and even treble stacking being resorted to, but the arrangement of the books leaves much to be desired. The matter has been taken up by the Library Committee, largely at the instigation of the Botanical Secretary, and work is actively in progress with the object of reclassifying and rearranging the books and journals, so as to group them as far as possible according to subjects, and thus make the Library much more easy to consult. This is a biggish task, and there still remains outstanding the problem of getting more shelf-space, which must be seriously tackled after the war.

Very great progress has been made in the photographing of the Linnaean Collections and Manuscripts; the work has, in fact, been very nearly completed. You will remember that we received a munificent grant from the Carnegie Corporation of New York for this purpose, which has enabled us to make a thoroughly satisfactory job of this big undertaking.

I include here the greater part of a progress report prepared by Mr. Savage, in March of this year, and sent to the Carnegie Corporation for their information.

Upon receiving notification from the Carnegie Corporation of New York that a grant of \$8,060 had been allocated for this purpose, the Council of The Linnean Society of London appointed a Committee for the Photographing of the Linnaean Collections, of which the following were members : Dr. J. Ramsbottom (Chairman), Mr. A. J. Wilmott, Mr. J. R. Norman, Mr. J. E. Dandy, Mr. S. Savage, Mr. W. H. T. Tams, Dr. Malcolm Smith and Mr. I. H. Burkill. At its first meeting, held 12 June 1941, estimates were considered and the decision taken that the record should be made on 35 mm. film, as the employment of the older plate-photography would have resulted in recording only about one-sixth of the essential specimens and no manuscripts. It was also decided to accept an estimate submitted by Messrs. Wallace Heaton, Ltd., New Bond Street, London, W. 1, for making about 60,000 photographs on 35 mm. film and supplying positives of the whole film and additional negatives.

The Collections were moved from Woburn Abbey to the Zoological Museum, Tring, Hertfordshire, and the work was begun in July, 1941. In the first place, Linnaeus's Herbarium, comprising about 14,200 sheets was dealt with ; and Mr. S. Savage numbered the sheets in accordance with Dr. Daydon Jackson's manuscript Catalogue, and did many necessary minor repairs to the specimens. The negative films were then submitted in batches and checked by Mr. Savage against the Catalogue. Omissions and faulty photographs were then made good.

Mr. W. H. T. Tams, Assistant Keeper, Department of Entomology, British Museum (Natural History), spent a number of weeks at Tring Museum preparing the whole of the Insecta for photographing. Mr. J. R. Norman, Deputy Keeper, Department of Zoology, British Museum (Natural History), gave much time to the preparation of the Mollusca for photographing, and in this was helped by the advice of Mr. A. E. Salisbury, an authority on that group. Mr. Norman also superintended the photographing of the Fishes. The number of photographs needed of the Insecta and Mollusca fell below that estimated, as it was found better in some instances to photograph two or more specimens together.

The important annotated copies of Linnaeus's own works were next selected and photographed. These were followed by the more important of Linnaeus's own manuscripts. In making these selections the Assistant Secretary endeavoured to include those manuscripts which were in some way directly connected with the Linnaean specimens. The work on the remaining large section of annotations—those of Linnaeus in the works of other authors—is still in progress and should be completed in a month or so. It was found desirable, and indeed necessary, to have a film of moderate length prepared of specimens of the handwritings of those who had sent specimens to Linnaeus, and to add any lists of such specimens, when available.

In this part of the Collections also, it was extremely difficult to estimate in advance the number of photographs : as many pages of an annotated book can sometimes be photographed as openings of two pages each. The final number is likely to be about 40,000 photographs.



The constant and detailed use of Dr. Daydon Jackson's manuscript Catalogue of the Herbarium brought to light many of its omissions and mistakes. The Assistant Secretary has spent and is spending a considerable amount of time in carrying out a revision of the Catalogue, which in some form is necessary, since genera in the film are divided only by numbers. At present, the inscriptions on the versos of the Herbarium sheets have not been photographed or fully copied. The Committee has deferred deciding whether to have the corrected Catalogue filmed or to recommend that a printed Catalogue should be put in hand, until it is seen more clearly what the unexpended balance of the grant is likely to amount to.

Through Dr. E. D. Merrill, lists of specimens of North American plants of which large-sized photographs are desired by United States of America herbaria were received, for which it was evident that an expenditure of £20 would be necessary. The Committee has recommended that these prints should be supplied through Dr. Merrill, provided that the balance of the grant was sufficient.

It was further decided to recommend that from any unexpended balance of the grant, after this and the filming or printing of the Catalogue of the Herbarium had been provided for, to distribute extra copies of the film (or part of it) more with the idea of the propagation of knowledge than of preserving a record of Linnaeus's work.

In the meantime, Messrs. Wallace Heaton, Ltd., had been experimenting in the production of *duplicate* negatives (i. e., a negative made from a positive obtained from the original negative), which showed that duplicate 35 mm. film negatives were very inferior in the smaller details of the photographs. The Committee then decided that, instead of duplicate negatives, twelve positive films should be distributed: especially as it was proved that quite satisfactory duplicate negatives from 35 mm. film are obtainable by using photographic plates of half or quarter-plate size.

A provisional recommendation by the Committee about the distribution of the film has not yet been fully discussed by the Council. No decision will be taken until the photography is completed, but the following list is given as an indication of what the members of the Committee have in mind:—

Linnean Society, 1 positive, and the original negative; British Museum, 1 positive; United States of America, 2 positives (Harvard and Smithsonian Institution, Washington): Canada, Australia, South Africa, India, Sweden, China, Russia, New Zealand and South America, 1 positive each.

I take this opportunity of expressing the warm thanks of the Society to all members of the Committee appointed for the purpose of organizing and supervising the photographing of the collections. They have done excellent work, and devoted a great deal of time and labour to their task. The grateful thanks of the Society are also due to the Trustees of the British Museum (Natural History) for giving facilities for the photography and housing the collections at the Tring Museum. How well the films have turned out we had an opportunity of seeing when Mr. J. R. Norman showed us some samples at the meeting held on 27 November 1941.

It should be mentioned that the Salmon Collection of birds' eggs, which has been in the possession of the Society since 1862, has been transferred to the British Museum (Natural History).

On staff matters—we regret the departure for war work of Miss Liddle, who filled the post of Assistant Clerk with much efficiency. For the time being, in the interests of economy, no appointment is being made to the vacancy. As the Deputy Treasurer has told us, after very careful enquiry made on their behalf by Mr. D. M. Reid and Dr. B. Barnes, the Council decided to expend the greater part of the accumulated Pension Fund in the purchase of Deferred Annuities for Mr. Savage and Mr. Warton, which will ensure for them modest pensions when they retire. The retiring age has been fixed at 65, and a scheme of contributory pensions for new entrants to the staff is proposed for the future.

On the financial state of the Society, which is set out in the Accounts circulated to you, the chief thing to record is that the payments in respect of War Damage Insurance have been a heavy drain on our resources, and have considerably reduced the amount of money that could be devoted to publications. We have been able during this first year to utilize the balance of the Herbert Spencer Fund and a legacy left us by the late Treasurer, Mr. Francis Druce, towards meeting this extraordinary and unavoidable expenditure, and it is satisfactory to know that the burden will be substantially less in future years. Our Treasurer, Major F. C. Stern, has, at his request, been given leave of absence, owing to the heavy demands made on his time by his responsibilities of command in the Home Guard, and the Council record with gratitude that Dr. Barnes has undertaken the duties of Deputy Treasurer and carried them out most ably.

The Society has received by bequest from Sir Arthur Evans, a portrait of Ehret, and under the Will of the late Mr. R. J. Flintoff, a sum of £1,000 will accrue after the death of two intermediate beneficiaries. A generous gift has been made to us by Dr. T. Wayland Vaughan, one of our Foreign Members, from the sale of his medals; and from America also has come the tea, sent by Dr. E. D. Merrill and Dr. Thomas Barbour, which we have enjoyed after our meetings. I have referred already to the legacy (£200) from Mr. Francis Druce. The Society has also greatly benefited by the bequest of a selection of his Library. Apart from many works of ordinary interest which escaped the fire at Mr. Druce's flat, about 20 works of greater value, which Mr. Druce had had stored in safe keeping, have come to the Society and are now in safety at Tring. Included is a fine copy of *The Grete Herball*, printed in Southwark in 1526, a copy of the first edition of Parkinson's *Paradisus*, 1629, and other early herbals; as well as a very rare edition of Linnaeus's *Amoenitates Academicæ*, dated 1786 (Coloniæ-Allobrogum).

This year, for the first time, there will be no award of the Linnean Gold Medal. It is impossible to obtain the necessary gold, and the Council came to the conclusion that it would not be worthy of the Society's traditions to offer a medal of silver gilt. The award must therefore await those happier days, which we can already see dawning upon us.

In conclusion, I should like to express my grateful thanks to the Botanical and Zoological Secretaries and to the Deputy Treasurer for the very great assistance they have rendered to the Society and to myself during the year.

## TREASURER'S ACCOUNTS FOR THE

(Presented at the Anniversary

*Receipts and Payments of the Linnean Society*

|                                                                                                                                                        | RECEIPTS | £ s. d.  | General | £ s. d. |
|--------------------------------------------------------------------------------------------------------------------------------------------------------|----------|----------|---------|---------|
| To Balance at 30 April 1941 :—                                                                                                                         |          |          |         |         |
| Current Account at Bank .....                                                                                                                          |          | 241 8 11 |         |         |
| Deposit Account Post Office Savings Bank .....                                                                                                         |          | 1156 5 3 |         |         |
| Deposit Account Post Office Savings Bank (Herbert Spencer Fund) ...                                                                                    |          | 243 14 9 |         |         |
| Cash in hand .....                                                                                                                                     |          | 3 0 11   |         |         |
|                                                                                                                                                        |          |          | 1644    | 9 10    |
| „ Admission Fees .....                                                                                                                                 |          |          | 32      | 0 0     |
| „ Arrears of Annual Contributions .....                                                                                                                |          | 78 10 0  |         |         |
| „ Annual Contributions for year .....                                                                                                                  |          | 2019 0 0 |         |         |
| Do, in advance .....                                                                                                                                   |          | 44 0 0   |         |         |
|                                                                                                                                                        |          |          | 2141    | 10 0    |
| „ Interest on Investments (including Income Tax recovered) .....                                                                                       |          |          | 283     | 16 3    |
| Do. Deposit .....                                                                                                                                      |          |          |         | 17 10   |
| Do. Post Office Savings Bank Account .....                                                                                                             |          |          | 31      | 14 6    |
| „ Sales of Publications :—                                                                                                                             |          |          |         |         |
| Transactions .....                                                                                                                                     |          | 29 3 6   |         |         |
| Journals .....                                                                                                                                         |          | 44 1 3   |         |         |
| Proceedings .....                                                                                                                                      |          | 11 7 11  |         |         |
|                                                                                                                                                        |          |          | 84      | 12 8    |
| „ Donations in aid of Publications .....                                                                                                               |          |          | 100     | 0 0     |
| „ Donations for General Purposes (including bequest, £200, from the late Mr. Francis Druce, and £14 0s. 10d. from Dr. Wayland Vaughan, F.M.L.S.) ..... |          |          | 216     | 1 10    |
| „ Miscellaneous Receipts .....                                                                                                                         |          |          | 39      | 2 10    |
| „ £1200 India 3 per cent. Stock, acquired by H.M. Treasury .....                                                                                       |          |          | 1089    | 13 0    |
| „ Sale of £1599 2s. 0d. 3½ per cent. Conversion Stock (Staff Pension Fund) .....                                                                       |          |          | 1690    | 17 0    |
| „ Sale of £300 19s. 11d. 3 per cent. War Stock (Staff Pension Fund) .....                                                                              |          |          | 301     | 5 3     |

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 £7656 1 0

## Library

|                                                                  | RECEIPTS | £ s. d.   |
|------------------------------------------------------------------|----------|-----------|
| To Balance 1 May 1941 .....                                      |          | 287 16 11 |
| „ Interest on Investments (including Income Tax recovered) ..... |          | 43 0 8    |
| „ Donation .....                                                 |          | 3 0 0     |
| „ Deposit Account Interest .....                                 |          | 14 11     |
|                                                                  |          |           |
|                                                                  |          | £334 12 6 |

## Fellows Postal

|                                | RECEIPTS | £ s. d. |
|--------------------------------|----------|---------|
| To Balance at 1 May 1941 ..... |          | 50 7 1  |
| „ Deposits during year .....   |          | 2 1 0   |
|                                |          |         |
|                                |          | £52 8 1 |

YEAR ENDED 30 APRIL 1942

Meeting, 28 May 1942.)

from 1 May 1941 to 30 April 1942.

**Account**

|                                                                                            | PAYMENTS | £    | s. | d. | £            | s.       | d.       |
|--------------------------------------------------------------------------------------------|----------|------|----|----|--------------|----------|----------|
| By Coal, Electric Current, and Gas .....                                                   |          |      |    |    | 79           | 0        | 4        |
| „ Repairs : Sundry .....                                                                   |          |      |    |    | 2            | 15       | 7        |
| „ Taxes and Insurance .....                                                                |          |      |    |    | 58           | 4        | 2        |
| „ Miscellaneous Printing and Stationery .....                                              |          |      |    |    | 93           | 11       | 2        |
| „ Petty Expenses and Postages .....                                                        |          |      |    |    | 160          | 12       | 7        |
| „ Fire Watching Expenses .....                                                             |          |      |    |    | 70           | 18       | 10       |
| „ Publications :—                                                                          |          |      |    |    |              |          |          |
| Printing .....                                                                             |          | 441  | 5  | 5  |              |          |          |
| Illustrations .....                                                                        |          | 29   | 5  | 9  |              |          |          |
| Distribution .....                                                                         |          | 38   | 14 | 7  |              |          |          |
|                                                                                            |          |      |    |    | 509          | 5        | 9        |
| „ Salaries, Wages, etc. (including £44 12s. 5d. Travelling Allowances) .....               |          |      |    |    | 1196         | 18       | 2        |
| „ Freshwater Biological Association Donation .....                                         |          |      |    |    | 5            | 5        | 0        |
| „ Linnean Medal .....                                                                      |          |      |    |    | 17           | 10       | 0        |
| „ Removal of Linnaean Collections .....                                                    |          |      |    |    | 18           | 15       | 0        |
| „ War Damage Insurance (Library, Furniture and Fittings) :—                                |          |      |    |    |              |          |          |
| Balance of Herbert Spencer Bequest .....                                                   |          | 243  | 14 | 9  |              |          |          |
| Balance paid from General Fund ..                                                          |          | 418  | 15 | 3  |              |          |          |
|                                                                                            |          |      |    |    | 662          | 10       | 0        |
| „ Purchase of £196 9s. 10d. 3 per cent. War Stock (Staff Pension Fund) [Since sold.] ..... |          |      |    |    | 200          | 0        | 0        |
| „ Purchase of £200 0s. 0d. 3 per cent. Saving Bonds (Staff Pension Fund) .....             |          |      |    |    | 200          | 0        | 0        |
| „ Purchase of £1089 13s. 0d. 3 per cent. Saving Bonds .                                    |          |      |    |    | 1089         | 13       | 0        |
| „ Staff Annuities (Single Premiums) .....                                                  |          | 1700 | 19 | 3  |              |          |          |
| „ „ „ (First Annual Premium). .....                                                        |          | 100  | 0  | 0  |              |          |          |
|                                                                                            |          |      |    |    | 1800         | 19       | 3        |
| „ Balance at 30 April 1942 :—                                                              |          |      |    |    |              |          |          |
| Current Account at Bank .....                                                              |          | 155  | 5  | 5  |              |          |          |
| Deposit Account Post Office Savings Bank .....                                             |          | 1330 | 0  | 0  |              |          |          |
| Cash in hand .....                                                                         |          | 4    | 17 | 9  |              |          |          |
|                                                                                            |          |      |    |    | 1490         | 3        | 2        |
|                                                                                            |          |      |    |    | <u>£7656</u> | <u>1</u> | <u>0</u> |

**Account**

|                                                    | PAYMENTS | £   | s. | d. | £           | s.        | d.       |
|----------------------------------------------------|----------|-----|----|----|-------------|-----------|----------|
| By Periodicals .....                               |          |     |    |    | 61          | 18        | 4        |
| „ Binding .....                                    |          |     |    |    | 33          | 11        | 3        |
| „ Balance at 30 April 1942 : Current Account ..... |          | 89  | 2  | 11 |             |           |          |
| Deposit Account .....                              |          | 150 | 0  | 0  |             |           |          |
|                                                    |          |     |    |    | 239         | 2         | 11       |
|                                                    |          |     |    |    | <u>£334</u> | <u>12</u> | <u>6</u> |

**Account**

|                                     | PAYMENTS | £          | s.       | d.       |
|-------------------------------------|----------|------------|----------|----------|
| By Postages, etc. during year ..... |          | 1          | 4        | 0        |
| „ Balance at 30 April 1942 .....    |          | 51         | 4        | 1        |
|                                     |          | <u>£52</u> | <u>8</u> | <u>1</u> |



## RECEIPTS

| £    | s. | d. | £    | s. | d. |
|------|----|----|------|----|----|
| 10   | 10 | 0  | 10   | 10 | 0  |
| 482  | 6  | 3  | 482  | 6  | 3  |
| 57   | 13 | 5  | 57   | 13 | 5  |
| 1856 | 4  | 5  | 1856 | 4  | 5  |

\* The Bank of England holds £29 11s. 0d., dividends on Stock sold.

Market Value  
30 April 1942

General Account

| £    | s. | d. |                                                                 | £     | s.   | d.   |
|------|----|----|-----------------------------------------------------------------|-------|------|------|
| 1000 | 0  | 0  | 3½ per cent. London County Consolidated Stock 1938-38           | @106  | 1060 | 0 0  |
| 1000 | 0  | 0  | Eastern Bengal Railway 4 per cent. Irredeemable Debenture Stock | @ 97  | 970  | 0 0  |
| 1000 | 0  | 0  | Great Western Railway 4 per cent. Debenture Stock               | @113½ | 1135 | 0 0  |
| 312  | 0  | 0  | London Midland & Scottish Railway 4 per cent. Preference Stock  | @ 73  | 227  | 15 2 |
| 338  | 6  | 8  | 3½ per cent. War Stock                                          | @104½ | 353  | 11 2 |
| 1000 | 0  | 0  | 3 per cent. Defence Bonds                                       | @100  | 1000 | 0 0  |
| 2199 | 18 | 6  | 4 per cent. Australian Stock 1961-64                            | @ 89½ | 2188 | 18 6 |
| 200  | 0  | 0  | 3 per cent. War Stock 1955-59                                   | @100½ | 201  | 0 0  |
| 1139 | 13 | 0  | 3 per cent. Savings Bonds 1955-65                               | @100½ | 1141 | 1 6  |
|      |    |    |                                                                 | £8277 | 6 4  |      |

Library Account

| £   | s. | d. |                                                                   | £     | s.  | d.   |
|-----|----|----|-------------------------------------------------------------------|-------|-----|------|
| 450 | 0  | 0  | Forth Bridge Railway 4 per cent. Stock (Bentham Bequest)          | @103½ | 465 | 15 0 |
| 530 | 0  | 0  | East Indian Railway 3½ per cent. Debenture Stock (Tagart Bequest) | @ 85  | 450 | 10 0 |
| 103 | 12 | 5  | Surrey County 3 per cent. Stock 1961-66 (Wakehurst Bequest)       | @ 98  | 101 | 11 0 |
| 191 | 12 | 7  | 4 per cent. Australian Stock 1961-64 (Walker & Morey Bequests)    | @ 99½ | 190 | 13 5 |
|     |    |    |                                                                   | £1208 | 9 5 |      |

Separate Account

|          |    |           | Separate Account                                                  |       |                       |       |
|----------|----|-----------|-------------------------------------------------------------------|-------|-----------------------|-------|
| £        | s. | d.        |                                                                   |       |                       |       |
| £1063 10 | 7  | 232 5 0   | Metropolitan Water Board 3 per cent. "B" Stock (Westwood Bequest) | ..... |                       |       |
|          |    | 667 14 2  | Ditto                                                             | ditto | (Hooker Lecture Fund) | ..... |
|          |    | 163 11 5  | Ditto                                                             | ditto | (Goodenough Fund)     | ..... |
| £315 4   | 5  | 100 0 0   | New South Wales 3½ per cent. Stock, 1930-50 (Trail Award Fund)    | ..... |                       |       |
|          |    | 409 11 1  | 2½ per cent. Consolidated Stock (Cripp Award Fund)                | ..... |                       |       |
|          |    | 129 10 6  | India 3½ per cent. Stock 1931 (Westwood Fund)                     | ..... |                       |       |
|          |    | 61 18 0   | Ditto                                                             | ditto | (Hooker Lecture Fund) | ..... |
|          |    | 123 15 11 | Ditto                                                             | ditto | (Goodenough Fund)     | ..... |
|          |    | 200 0 0   | 3 per cent. Savings Bonds 1955-65 (Staff Pension Fund)            | ..... |                       |       |
|          |    |           |                                                                   |       |                       |       |

B. BARNES, Deputy Treasurer.

We have (in conjunction with the Professional Auditors, who certify as to all details) audited the Accounts of the Society for the year ended 30 April 1942, and found them correct. We have verified the Investments and Bank Balances.

Dated this 13 May 1942.

W. B. KEEN & Co., Chartered Accountants,  
224 Regent Street, London, W.1.

E. S. RUSSELL, I. GORDON.  
E. M. WAKEFIELD, I. HENRY BURKILL,  
D. M. REID. }  
Audit Committee

The PRESIDENT then delivered his Address, 'Perceptual and sensory signs in Instinctive Behaviour'.

On its conclusion, Professor F. E. WEISS, F.R.S., moved 'That the President be thanked for his excellent Address, and that he be requested to allow it to be printed and circulated amongst the Fellows'. The motion was seconded by Professor E. J. SALISBURY, C.B.E., F.R.S., and being put to the meeting was carried with acclamation.

The Scrutineers of the Ballot, who had retired at the appointed times with the voting-lists for the election of the Council and of the Officers, having completed their scrutiny, reported to the President, and he declared the result as follows :—

COUNCIL FOR 1942-43.—Dr. B. Barnes, Prof. F. T. Brooks, F.R.S., Mr. I. Henry Burkill, Mr. R. H. Burne, F.R.S., Dr. G. S. Carter, Mr. J. E. Dandy, Dr. E. Marion Delf, Dr. F. C. Fraser, Mr. A. C. Gardiner, Prof. T. M. Harris, Mr. C. C. Hentschel, Dr. N. A. Mackintosh, Dr. R. Melville, Prof. T. G. B. Osborn, Mr. J. R. Norman, Dr. J. Ramsbottom, O.B.E., Mr. Douglas M. Reid, Dr. E. S. Russell, O.B.E., Dr. Malcolm A. Smith and Major F. C. Stern, O.B.E., M.C.

(The retiring Councillors were Mr. J. S. L. Gilmour, Dr. Anna B. Hastings, Mr. H. R. Hewer, Dr. C. F. A. Pantin and Mr. H. W. Parker.)

OFFICERS FOR 1942-43.—*President*: Dr. E. S. RUSSELL, O.B.E., *Treasurer*: Major F. C. Stern, O.B.E., M.C.; *Deputy Treasurer*: Dr. B. Barnes; *Botanical Secretary*: Mr. I. Henry Burkill; *Zoological Secretary*: Dr. Malcolm A. Smith.

The President then announced that he appointed the following as the Vice-Presidents for 1942-43,—Dr. B. BARNES, Dr. G. S. CARTER, Mr. DOUGLAS M. REID and Major F. C. STERN, O.B.E., M.C.

## PRESIDENTIAL ADDRESS.

By E. S. RUSSELL, O.B.E., M.A., D.Sc.

## PERCEPTUAL AND SENSORY SIGNS IN INSTINCTIVE BEHAVIOUR.

I pointed out in my Address last year (Russell, 1941) that valent objects are often distinguished in perception by means of a few characteristics, such as a specific smell, size or shape, the heat radiated from them, or their mode of motion. These distinguishing characteristics, to which the animal is instinctively predisposed to attend, I called perceptual clues or signs, and I tried to show that such signs were normally adequate as indicating the biologically appropriate object.

I propose to pursue this subject a little further, by bringing together a number of examples illustrating the simplicity and normal adequacy of these perceptual signs, which play such an important rôle in instinctive behaviour, and I shall begin by considering the valence of moving objects.

By many animals of 'visual' type, objects seen to be in motion are treated as potential food, provided they are neither too small nor too large. This is true especially of animals that feed on living and active prey, of carnivores and insectivores particularly, and does not hold good of grain-feeders, grass-croppers and vegetarian animals generally.

How far perception of form also enters into the matter is difficult to decide, for the response is to an object that moves, to a moving image, and it is impossible to dissociate completely perception of motion from perception of form. But the evidence presented in the following pages tends to show that for many predatory animals of visual type their prey is not primarily an object of specific shape and pattern, such as it appears to us, but merely something, of certain dimensions, that moves. The behaviour of a kitten or a puppy illustrates this well; both will stalk or chase any small moving object whatever it may be.

Among birds, a good example of the food-valence of moving objects is provided by the shrikes (*Lanius*). They are carnivorous in habit, eating all manner of small prey—mammals, birds, reptiles and insects—provided they are neither too small to be worth picking up nor too large to be mastered.

From Miller's admirable monograph of the American shrikes (1931) I take the following description of their feeding habits:

Animals which are captured, it is believed, are located largely by the detection of their motion, either in the air or on the ground, but principally the latter. In captive birds any flying, crawling, or moving thing draws attention and usually pursuit. Thus, a dead mouse is far less exciting to a shrike than a live mouse. Moths or flies in the cage are pursued vigorously. In adults, until it is learned that a particular kind of inanimate object is edible, such an object is not often picked up in the bill. On the other hand, both captive and wild birds are curious and engage in a certain amount of inspection of stationary objects. . . . Immature birds, particularly, pick up and investigate the edibility of motionless things. One captive juvenile swallowed string and rubber bands which were lying in its cage, eventually disgorging them as pellets,



Evidently, a shrike to some degree learns to recognize suitable food materials by "trial and error". However, *anything that moves rarely proves to be unsuitable food and an adult uses motion as the most reliable criterion of food* (pp. 210-11, our italics).

Moving objects may indeed act with 'imperative' valence, and cause the bird to pick them up even when it is too full to eat them. 'The bird is so constructed', writes Miller, 'that it must capture moving objects, and the intensity of this reaction is affected only to a moderate degree by actual hunger' (p. 218). When the food has been seized the shrike proceeds to impale it on a thorn or other suitable projection, preparatory to tearing it up with the beak; in the bird that is not hungry the series of actions ceases with the impaling.

For many raptorial birds, such as hawks and buzzards, motion is the primary food-valent characteristic (Brüll, 1937), and moving objects may be seen and responded to at very great distances. Bastian Schmid, who carried out some experiments with a pair of peregrine falcons, found that one responded to a lure waved in the air at a distance of 1,661 metres, though visibility was not very good. The other noted and flew towards some pigeons foraging in a field 1,077 metres away, though their movements were slow and inconspicuous to the human eye even when aided by binoculars (1936, p. 64).

Young birds of many kinds, as Lloyd Morgan pointed out (1896, p. 46), are attracted by small moving objects, such as insects and caterpillars, and peck at them. (Large moving objects generally have danger valence.) Protective coloration is of little avail if the insect moves. Thus the clear green caterpillar of *Pieris rapae* on a nasturtium leaf was picked off by Lloyd Morgan's moorhen chick the moment it moved its head, and young stick insects on lime leaves were snapped up directly they showed signs of life. This was Stockard's experience (1908) also with the 'walking stick' insect *Aplopus mayeri*, which is nearly invisible when it rests immobile during the day, hanging to grass stems or twigs. Specimens placed on the ground near a hen with chicks attracted no attention till they began to move, when the hen approached and seized them.

In his experiments on the protective coloration of insects, carried out with caged birds, Young (1916) found that motionless food was often ignored by his birds, whether it was conspicuous or not, while moving food usually attracted them. His general conclusion was that 'stillness is probably a more important factor than colour in protecting animals from their foes'. He holds that hovering hawks are induced to swoop and pounce by the motion of their prey, and not by its form and pattern.

It is indeed the general experience of those who have experimented with birds and protectively coloured insects that the value of the protection is immediately destroyed when the insect moves. Thus Carrick (1936) found that the caterpillars of *Selenia bilunaria*, which closely resemble twigs, were quite unnoticed by wrens and warblers, which repeatedly perched on the hawthorn branch on which they were standing rigid and motionless, but that any movement was apt to prove fatal to them. He noticed on many occasions throughout his experiments, which were carried out in the field, that it was the *moving* insect that attracted the attention of the bird.

'The importance of stillness as an aid to concealment', writes Cott (1940, p. 161), 'can hardly be overestimated. Once movement occurs, the best cryptic devices tend to become ineffectual'.

The North American whip-snake (*Zamenis*), according to Gettkandt (1931), responds, if hungry, to almost any moving object in its vicinity, so it be not too large, by trying to seize it. His experiments show that the following objects in motion attract its attention and at least the beginnings of the feeding response—mice sitting washing themselves or fidgeting about, mice running away, fluttering sparrows, slowly creeping lizards, its own kind, and even a human hand moved slowly by. If the moving object is large—more than the length of a man's forearm—or exhibits sudden movements, as a frog jumping, the snake flees from it. (It is said not to eat frogs.) The form and colour of the prey appear to be unimportant, and the snake will strike at the blurred image of a small animal seen through thick glass. Its natural prey consists of small rodents or birds or even its own kind; it also eats eggs, so that motion is not its sole criterion of food.

Most snakes in captivity must be fed on living or moving prey. 'Even if they will eat dead animals, these animals must be moved about in the semblance of life before their presence is appreciated' (Wood-Jones and Porteus, 1929, p. 265).

An interesting observation showing the stimulating effect of moving objects is reported by Burgess Barnett ('Field', Jan. 13, 1934, p. 71), who writes, 'It was found possible to rear vipers from birth by giving them strips of frog-meat on forceps, but that they would only feed if their feeding reflex was stimulated at the same time by the sight of a living frog beyond a glass partition in the cage. The frog had, however, to be almost small enough for the little creatures to swallow; if it were too large the fear reflex was excited, and several hours had to elapse before they could be induced to feed again'.

For many Amphibia, and especially the Anura, small moving objects have food-valence, and motionless prey elicits no response. Franz (1927) found with respect to the common frog (*Rana temporaria*) and the natter-jack toad (*Bufo calamita*) that even after they had been fed on mealworms for months they paid no attention to the motionless larva but snapped it up when it started to crawl. The response is not limited to food objects. Fire-bellied toads (*Bombina*) which I kept in a glass tank would follow and bite not only at moving insects inside or outside the walls, but also at an end of rubber tube moved past them slowly. They would snap at a moving salamander (*S. atra*), and pay attention also to a blade of grass set in motion by it.

A small moving object may indeed act with compelling force, with 'imperative' valence, bringing about the feeding reaction far beyond the needs of the animal. A striking illustration of the imperative nature of the stimulation is recalled by Maier and Schneirla (1935), who write 'The frog is so strongly compelled to snap at any small moving object that in an experiment by Abbott (1862) an individual severely injured its jaws by repeatedly lunging and snapping at a fly pinned in the centre of a ring of needles. In such cases the fly does not stimulate as "food", but as a small moving object, a visual stimulus of powerful coerciveness' (p. 202).

With the opinion expressed in the last sentence I can hardly agree ; a small moving object has undoubtedly food-valence.

Motion is not the only cue eliciting the feeding response in Amphibia. Smell and water-vibration come into play in many Urodela ; tactile stimulation, and probably hearing, may come into the story in some Anura. Franz, for instance, reports (1927) that *Bufo calamita* will respond to a mealworm, outside its field of vision, which comes in contact with its hind quarters or hind leg ; the toad will then turn round and seize the mealworm. *Rana temporaria*, on the other hand, did not show this response. According to Maier and Schneirla (1935) the rustle of leaves will cause the toad to take up an attitude of readiness to seize prey. I have observed in *Bombina* approach to a wriggling worm which was not visible ; the stimulus was presumably an auditory one.

When a small object is moved across the field of vision of a young *Amblystoma* larva it turns first its head and then its whole body to follow the moving thing. This is the first act of attention which it shows—an act of the body as a whole—and it is followed either by a slow advance towards the object in motion or a spring as if to capture it (Coghill, 1936).

The 'fighting fish' (*Betta splendens*) treats any small moving object as possible food, snapping even at sinking grains of sand or at drops of moisture slipping down the outside of the aquarium wall (Lissmann, 1932). Form and colour are unimportant ; any moving object is liable to be seized, if it is not too big to be taken in the mouth ; taste and possibly tactile sense determine whether it is swallowed. It is a purely visual feeder, and does not feed in the dark. Water disturbance, setting up local currents, merely arouses general attentive behaviour and exploratory movements, which may turn into feeding behaviour, defence reactions or sex behaviour, according to the nature of the object causing the disturbance ; localized water-movement therefore does not possess immediate food-valence, as it does in some other animals (see p. 203).

While *Betta* as a rule is restricted to moving food, it will, if very hungry, pick up conspicuous fragments from the bottom.

The three-spined stickleback (*Gasterosteus aculeatus*) also is attracted by any small object in active motion or falling through the water, and takes it up in the mouth, to swallow or reject, as the case may be. But it will also seize motionless objects ; form perception comes into the story (Russell, 1931).

Miss Lebour (1919) tells us that post-larval whiting (*Gadus merlangus*) will not touch dead copepods, and that young lumpsuckers (*Cyclopterus lumpus*) will chase their food only if it is moving. Thus when a young *Cyclopterus* attacks a large *Idotea* and the *Idotea* 'feigns death', the attacks cease until the *Idotea* begins to move again, when it is immediately pursued.

That many kinds of fish are attracted by a moving object is demonstrated by the successful use by the angler fish (*Lophius piscatorius*) of its lure. This is a tag of skin on the tip of the long first dorsal ray. When fish are about and the angler is hungry it erects this fishing rod and jerks the lure rapidly to and fro. 'The moving lure has a strong attraction for healthy hungry fishes of several kinds. Small pollack, whiting, pout, and bass were the species actually observed to be attracted to it, but



probably most pelagic fish that capture moving prey by sight would at least swim up to investigate the darting object. Many fishes take a ready interest in moving things' (Wilson, 1937).

The human angler takes advantage of this in many ways, as when he trolls with some bright coloured object as a lure.

The solitary wasp *Philanthus triangulum* provisions its nest exclusively with honey bees, which it catches on the wing. The careful observations and experiments of Tinbergen (1932, 1935) have shown that the bees are found by a simple combination of optical and olfactory impressions. Flying over its hunting grounds the wasp is attracted to any bee or similar insect moving through the air within about 30 cm. of it; it orientates towards the insect, flies near to it, generally up-wind, and hovers at a distance of 5-15 cm., taking its scent. If it is a humble bee or a fly or a beetle, it has no bee-scent and is generally left alone. If it is a bee the wasp makes contact with it, stings it, licks its honey and carries it off to its burrow. The 'formula' is therefore a simple one—any flying thing of approximately the right size is possible prey; discrimination between bees and other insects is made by smell. The proof of this interpretation is supplied by Tinbergen's experiments (especially 1935). The wasp is attracted to and hovers in front of freshly killed bees attached to a horizontal thread waving in the wind, also to dead bees deprived of their smell by being soaked in alcohol, attached in a similar way, and even to a little piece of twig suspended in like manner, whether these have been made to smell of bee or not. Motionless bees attached to twigs attract no attention at all. Sometimes in these experimental conditions the wasp makes contact with an object not smelling of bee, but never stings it or attempts to carry it off. But it will sting a fragment of twig which has been given a bee odour. In the experimental conditions described, the full reaction of seizing, stinging and carrying off (or attempted carrying off) is given only to the freshly killed bees. Flies given a bee odour by being rubbed over with freshly killed bees are attacked and stung, but not killed or carried off (1932, p. 327). The first part of the reaction then is determined entirely by optical impressions—anything, of suitable size, flying or moving in the air, attracts attention; if it has the specific bee smell, as determined by scenting it a little way off or by actual contact the reaction is continued, at least to the length of stinging the object. The completion of the action seems to depend on the object having certain other characteristics, probably perceived through the tactile sense, appertaining specifically to the bee. There is no optical recognition of the bee; it is recognized solely by its specific smell—in natural conditions a perfectly adequate and exclusive characteristic.

There is one exception to the rule that the wasp pays no attention to motionless bees, and that is when it has dropped or been forced to drop the bee it is carrying back to the nest. In these circumstances it will search for the bee on the ground, being guided in its search almost entirely by smell.

Most dragon-fly larvæ respond to moving objects as to food. Thus the larva of *Agrion* flicks out its labium towards any object in motion, provided this is not too big or moving too rapidly; the response is given whatever the object may be; it will react, for instance, to a moving needle.



It will also pick up motionless food, but only such as has just settled down after movement which the larva has watched (Alverdes, 1923). If, however, the larva is not hungry it may react to a moving needle or other object as to a possible enemy—the valence of the object changes.

Similar observations have been made by Sälzle (1932), who tells us that when the larva is hungry it will attempt to seize any small moving object within reach, whether this be a small *Oligochæt*, or a small plasticine or metal sphere fixed on the end of a wire. If the moving object is out of reach the larva either stalks it or waits till it comes nearer. On perceiving a small object in motion it orientates exactly towards it, and it rarely misses its strike.

The larva of *Aeschna* reacts even to objects in motion outside the glass walls of its aquarium—by flight if they are large, by orientating towards them if they are small (Gaffron, 1934). Under certain experimental conditions the larva can be induced to snap at a motionless object, if this is seen in apparent motion against a moving background.

The larva of the water-beetle *Dytiscus* shows the same sort of behaviour towards moving objects (Blunck, 1924). It reacts to any actively moving object in its vicinity by attack or by flight, according to size, perceiving large objects 5–10 cm. off, smaller things 2–5 cm. distant. Normally it lurks for its prey, leaping upon any small moving object that comes within its field of vision. Only if very hungry does it seek actively for prey. It will eat its own kind, but pays little attention to slowly moving animals like molluscs.

The wolf spiders, *Lycosidæ* and *Pisauridæ*, have eyes adapted for perception of motion rather than form (Homann, 1931). *Pisaura* turns towards all small moving objects, whether they be insect prey, or models of such, or even moving shadows. It will orientate towards small balls of black wax in motion, or to the moving end of a grass stem. To a motionless fly it does not respond, but let the fly move and it will be noticed, if it is not more than 10 cm. away. Once the spider's attention is aroused by a moving object it searches for it more or less blindly; form-perception is poor.

The land crab, *Ocypoda arenaria*, according to Cowles (1908), while it can see stationary objects, is much more attentive to objects in motion. It is attracted to little fish cast up on the beach by their dancing and flopping movements. If fish or chips of wood are thrown to it, the crab rushes up to seize or examine them. That vision of movement is the decisive thing is shown by an experiment of Cowles, where he suspended a fish by a thread 10 cm. over the sand; the crab approached, and failing to reach the fish, tried repeatedly to capture the moving shadow which it cast on the beach.

The food valence of 'moving objects of a certain size', which has been demonstrated in the examples described above, illustrates very well the simplicity of the perceptual field in instinctive behaviour and its adaptedness to the 'most usual' or 'most frequent' eventuality. Objects that move, especially with a translatory motion, are usually, though not always, alive; if an animal treats as possible prey any moving object of appropriate size the chances are that, in normal circumstances, it will not often be deceived; motion is normally sufficiently 'adequate' as a sign of

possible food. Decision as to the nature of the moving object when captured is made through smell or taste or some other sense.

It is interesting to note that size is important as well as motion—size relative to the predator. Moving objects above food-size may be treated as dangerous.

As we have already seen, objects which in motion have food valence may lose this valence when they cease to move; they merge into the 'neutral background' of action. The toad pays no attention to motionless mealworms, nor the young lumpsucker to an *Idotea* when it 'feigns death'. The value of immobility in escaping enemies is manifest.

So too, objects in motion or showing even slight movements, which are normally treated as danger-objects, may if quite motionless be totally unperceived. I have referred in my 'Behaviour of Animals' (1934) to the well-known fact that many wild animals will approach quite close to a motionless man without noticing him—'they are prone to walk almost on to him, without apparently having the smallest idea of his presence, notwithstanding that they may be gazing straight in his direction', says Stephenson-Hamilton (1912). Here is another example, taken from the Annual Report (1935) of the Tanganyika Game Preservation Department. 'On one occasion Captain Moore was standing in the middle of the road near to the Orangi drift, when from the opposite side of the drift appeared twelve Thomson's gazelle. As they walked towards the drift, he froze in his tracks to see what they would do. He was in full view, some twenty yards away, and wearing a light-coloured shirt. They actually crossed the drift and passed on either side of him within two feet so that he could have touched them, and it was not till they were twenty yards past him that they ran away'. He had merely 'obstacle' valence, as part of the landscape.

Further illustrations are given in a series of letters in 'The Field' for 1919, and here is one from Fraser Darling (1937) relating to the red deer. 'I stood', he writes, 'against the trunk of a birch, motionless. The deer had not seen me and they came slowly on, browsing at tufts of bents and heather which showed through the snow. The light was failing, but the snow and clear air helped to keep objects sharply visible. Three hinds and a stag approached the trees under which I stood. They rose on their hind legs and browsed on the twigs of the very one above me. I could have touched them and their breath came in my face. Many more of the herd were within five to twenty yards. I had the feeling of having reached that state which all watchers of animals desire, of having dispensed with my physical presence. The deer moved on in their grazing in twos and threes, and I was left alone under my tree in the still and silent air. They seemed to have been unaware of me only three feet away from them' (p. 187).

Objects seen to be *approaching*, especially if they are large and fast moving, are likely to have danger valence and to produce defensive or flight responses. If, hurrying to the telephone, I rush through a room where my dogs are playing, they may take fright and bolt to their beds. If I quietly approach a stream on the banks of which frogs are resting they see the large moving object and plop into the water. The phenomenon is, of course, well known and hardly requires illustration.

The danger valence of a *slowly approaching* object has been demonstrated by J. von Uexküll (1912, 1921) in his study of the behaviour of *Pecten*. Its chief enemy is the starfish *Asterias*, and it responds to the starfish's stealthy approach by directing its tentacles towards the creeping enemy, ready to flap away as soon as it perceives the specific scent of the starfish. Form and colour do not come into the story—it is highly improbable that the *Pecten* with its many eyes can form any definite image of the starfish—for it gives the same response to any approaching object, such as the human hand, provided its tempo of movement is closely similar to that of the starfish.

Here are two examples of the special valence of *receding* objects. The newly born lamb, as soon as it can stand on its feet, will follow any object moving away from it—its own mother, or a dog or a man on horseback (Hudson, 1892). 'I have seen', writes Hudson, 'a lamb, about two days old, start up from sleep, and immediately start off in pursuit of a puffball about as big as a man's head, carried past it over the smooth turf by the wind, and chase it for a distance of five hundred yards, until the dry ball was brought to a stop by a tuft of coarse grass'. A few days later the lamb begins to discriminate between different kinds of receding objects and learns to recognize its own mother. At first the mother-valence is extremely general—*any* object moving away,—so general as often to mislead the young lamb. But normally it works, for its mother is the most usual receding object which it encounters.

That at first its mother is not an individualized object recognizable as such is shown by the further observation of Hudson that the new born lamb will run from any object that approaches it, even its own mother. Such objects have danger valence.

According to Lorenz (1935), the newly hatched young of the grey lag goose (*Anser anser*) adopt as their parent the *first moving object* they see. If they are hatched in an incubator, and the first thing they see is a man they will accept him as their mother and follow him about; they will then refuse to have anything to do with adult birds of their own kind. Fraser Darling (1938) relates how a newly born gosling of this species adopted him as a foster parent.

'Moving objects of a certain size' may have mating-valence. Many male frogs and toads in the breeding season will seize and clasp any moving object of about their own size which they encounter. Sometimes the moving object is a fish, and the frog may clasp and hold on to it grimly, eventually killing the fish. As the sexes congregate together for breeding the moving object seized is usually another frog. If it is another male it is released, if a female the male frog cleaves to it. But, as Noble says, 'no male frog recognizes the female as a sexual object' (1931, p. 410). It discriminates female from male by certain simple qualities. In the American wood frog (*Rana sylvatica*) the main valent characteristic of the female is its girth and resistance to compression; Noble and Farris (1929) have shown that male frogs of this species injected with water until they have the same girth and firmness as a female with eggs, are treated as females, being seized and held as long as true females. A second valent characteristic of the female is its silence; the male frog, embraced by another of the same sex, croaks, the female in like circum-



stances is silent. So the male frog seeks not 'a female frog', but merely something of a certain size that moves'. When it has seized the object, other simple qualities which it perceives determine whether the male lets it go or holds on to it. These qualities are in normal circumstances quite adequate, enabling the frog to distinguish between the suitable and the unsuitable objects.

Objects in motion may be perceived through other senses than the visual. Often such objects give rise to disturbances or vibrations which are transmitted through the air or water or earth and give warning of their approach or passage. Such auditory or tactile messages usually have danger valence and elicit movements of defence or of flight, but in not a few cases they lead to feeding response or movements preparatory thereto.

I have given a number of instances in my book on animal behaviour (1934, pp. 33, 73-8, 116-17), the gist of which I may summarize here, adding, however, some additional examples. *Amoeba* and *Pelomyxa* feed in part upon flagellates and ciliates, which are sensed through the vibrations they set up in the water, and captured by means of pseudopodia thrown out and around them.

It has been shown by Schaeffer (1912-13) that for *Amoeba dubia* any small particle suitably agitated possesses food valence. 'All sorts of particles' he writes, 'whether digestible or not, are eaten if properly agitated'. Not only is it unnecessary for the agitated particle to lie in contact with the amoeba, but vibrations produced by a needle are likewise reacted to positively, if the needle point is one-fiftieth of a millimetre or more from the amoeba'. Such vibrated particles are never long retained, whether edible or not, for the vibration ceases when they are enclosed in the food cup, and their food valence disappears.

Sandon (1932) in his valuable account of the feeding habits of Protozoa quotes from Verworn the statement that both *Diffugia* and *Polystomella* react positively to and ingest inanimate objects set in motion, such as glass splinters or fibres of filter paper, remaining indifferent to them when they are at rest (pp. 67, 72). *Actinosphaerium* also 'will seize objects such as fibres of filter paper if the latter are suitably moved about, but not when they are motionless'. Even living organisms such as are seized whenever they swim actively against the pseudopodia do not call forth any response when motionless' (p. 76).

The freshwater leech *Piscicola geometra* 'attaches itself firmly by the posterior sucker to some convenient object, and, stretching itself out like a rod and swaying its body to and fro, lies in wait for its prey. With the anterior sucker it strikes at and fixes upon any passing fish with remarkable speed and precision, and, letting go its hold posteriorly, is carried off attached to its victim' (Harding, 1910, p. 142). Now *Piscicola* will become agitated and swing its head towards any localized disturbance of the water in its vicinity caused by the experimenter; water-disturbance or vibration is the valent characteristic eliciting the attempt to fix on its host. Similar behaviour is shown by the fish-leech *Hemiclepsis*, but not by other little leeches, such as *Glossosiphonia* and *Herpobdella*, which are not parasitic on fish; they respond to water disturbance by retraction.



Vibrations transmitted along the surface of water are perceived by certain insects and spiders and elicit food-getting responses. This is the case with the water-bug *Ranatra*. It lies in wait with its fore-legs stretched out, grabbing everything that touches them, but it also responds to objects passing near with which it does not come into contact. Thus, if it is hungry, touching the surface film with a needle will often cause it to feel around actively and attempt to seize what has caused the disturbance. Wolf-spiders of the genus *Pirata*, which are semi-aquatic, respond to ripples on the water as web-spiders do to vibrations of their web. The common species *P. piratica* lives at the edge of the water, spinning a tube on dry land in which to live. It sits in the mouth of this tube, with its fore-legs stretched out touching the water surface. If small insects are dropped upon the water, the spider rushes out and secures them, just as a web-spider runs across its web. Similarly, if the water be touched with the prong of a vibrating tuning-fork, *Pirata* will run forward to the fork (Savory, 1936).

It is a well-established fact that web-spiders are attracted to a fly caught in the web through the vibrations set up by its struggles. They will respond equally well to similar vibrations caused by bringing a tuning-fork in contact with the web, or some other rapidly vibrating object. Barrows, for instance (1915), used a vibrating straw; he found that the spider (*Epeira sclopetaria*) ran up to and bit the end of the straw; sometimes it spread a little silk over it, treating the vibrating object exactly as if it were a living fly. If the vibration lasts only a fraction of a second the spider orients towards it but does not rush up; the first part of the reaction—attention—may be the only one to take place.

In many web-spiders the male signals his approach to the female by setting up particular vibrations in the web which are different from those produced by normal prey. Here is Savory's account of the procedure (1935). 'Web spiders almost invariably pay court by sending messages along the threads of the web. The wandering male, on reaching the outskirts of a female's web, drums on it with his palpi or plucks at it so as to cause it to vibrate in some way which evidently does not affect the female in the same manner as do the vibrations set up by a captured fly' (p. 15). As a moving object on the web, causing vibrations, the male would have food-valence, did he not announce his mate-valence by these peculiar vibratory signals. After coitus he regains his normal food-valence and has to flee for his life.

I have referred at some length in my 'Behaviour of Animals' (pp. 116-18) to the characteristic feeding response given by young nestlings to the arrival of the parent bird. In many Passerine birds, especially those that nest in trees and bushes, any slight jarring of the nest or bough, such as is caused by the parent birds alighting, calls forth a feeding response even in very young and helpless nestlings; they raise their heads straight up and gape widely for food. The new born Californian Shrike (*Lanius ludovicianus*)—to take only one example—shows this response little more than an hour after it is hatched (Miller, 1931). It raises its head when it is touched or the nest is jarred. The mouth is opened, showing its conspicuous internal coloration, and 'faint thin notes, *tsp, tsp*, are given by the young as the head is held unsteadily upward'.

The response has been studied very thoroughly in the blackbird (*Turdus merula*) and the thrush (*T. ericetorum*) by Tinbergen and Kuenen (1939). Up to 10 or 11 days the nestlings react only to tactile or vibratory stimuli and the response is to raise the head vertically and gape. Shortly after the eyes are open the nestlings direct their beak towards the head of the parent bird, or to any object resembling it in contour.

We are concerned here only with the initial response, before the eyes are used. In this early period it is clearly established by Tinbergen and Kuenen that a light touch on the nest such as is caused by the alighting of the parent bird invariably calls forth the response, except immediately after feeding. Too strong a stimulus may elicit cowering instead of the raising of the head. Gently touching the fold of skin at the angle of the beak will generally induce the response, as will often gentle air currents, such as are produced by the approach of the parent bird.

It is of interest to note that, according to Lorenz, nestlings which live in holes do not give the feeding response to a tap near the nest, but exhibit, on the contrary, a fear response (1935, p. 182). But many of them do so in response to a darkening of the entrance (p. 194). This is not the case with the thrushes studied by Tinbergen and Kuenen, nor with the starlings investigated by Holzapfel (1939), though the latter nest in holes. Holzapfel, however, finds (p. 537) that nestling starlings do not respond to vibratory stimuli (to which they are not normally exposed in natural conditions), in contrast to the thrushes and other birds that rest in trees and bushes.

A curious parallel to the feeding response in young altricial nestlings is afforded by the behaviour of certain wasp larvae, of the genera *Belonogaster*, *Ropalidia* and *Polistes*. These are fed in their cells by the nurse wasps, who eagerly imbibe the abundant saliva produced by the grubs. The stimulus which leads the larvae to move up to the cell entrance, and protrude their mouths for food, an action accompanied usually by a flow of saliva, is provided by the rapid agitation of the bodies of the wasps and the vibrations of their wings. 'It is easy to provoke the secretion of the larvae artificially. Merely touching the borders of the mouth will bring it about. The forward movement of the larvae at the cell entrance, causing them to protrude their mouths to receive the food pellet, is also easily induced by vibration of the air in the neighbourhood of the nest. It is only necessary to whistle loudly or emit shrill sounds near a nest of *Belonogaster* to see all the larvae protrude their heads to the orifice of the cells' (Trans. by Wheeler, 1923, p. 84, from Roubaud). How these vibrations are perceived, whether by hearing or by 'feel', is not clear, but their valence is clearly the same as that of the jarring of the nest, or of the call note of the parent bird, which call forth the feeding attitude in nestlings.

A case where the original source of stimulation is a moving object (generally a living prey) the effects of whose motion are transmitted mechanically to the percipient animal, is provided by the ant-lion, the larva of *Myrmeleon*. When it is lurking at the bottom of its funnel of sand, any fall of material down the slope will cause it to flick sand vigorously up the sloping walls. If, as is likely, the disturbance is caused by a wandering insect, this action is calculated to bring it tumbling down within

reach of the ant-lion, and the objective intention of the flicking action is obviously to capture prey. Falling sand is in this case normally indicative of food to come, just as a touch on the nest indicates to the nestling thrush the approach of food.

Returning now to the visual field, we may note that the colour and shape of objects, as well as their movement and size, may be valent characteristics eliciting instinctive response. Here are one or two examples.

A Cichlid fish, *Hemichromis bimaculatus*, known as the jewel fish, develops in both sexes, during the breeding season, a reddish colour on the sides and lower surface of the head and part of the body. Both the male and the female guard the eggs, and also, for over a week, the young. The experiments of Noble and Curtis (1939) have shown that the young fry have an inborn or instinctive interest in red moving objects; they are attracted by a moving disc of this colour waved to and fro outside their tank, and they are not attracted by discs of other colours. In two species of *Cichlasoma*, on the other hand, which assume bluish black or black breeding colours, it was found that the fry were attracted much more to black or bluish black moving discs, and hardly at all to red or yellow. It seems, therefore, that these young cichlids are born with an innate disposition to follow moving objects of a certain size having the nuptial colour of their parents. This simple formula is normally adequate to ensure their keeping near the parents during early life. It has been shown, also by Noble and Curtis, that the red nuptial colour in *Hemichromis* is of importance in sex-recognition, and that the female exhibits a preference for highly coloured active males. It is not the colour *per se* that is attractive to the female, but the colour in combination with particular movements. 'The nuptial colours serve to render both the sex-identifying and the sex-stimulating movements of the male more conspicuous to the female' (p. 44). The nuptial colours also make intimidatory gestures conspicuous, and are thus of value in protecting the eggs and young.

That young Cichlid fish may have an instinctive predisposition to react to an object of a certain size and shape (normally the mother) is shown by the work of Peters (1937) on *Hemichromis* and *Tilapia*. Both *Tilapia natalensis* and *Haplochromis multicolor* are 'mouth breeders', and when the young hatch out they keep near the mother in a shoal. When the mother is alarmed, she turns towards the young and sucks them into her mouth. The young also swim actively towards the mother's mouth, and they will approach in the same way rough models with eyes, making for the position of the mouth.

The *Tilapia* female is much bigger than the *Haplochromis*, about 18 cm. in length, as compared with 5 cm., and it has a much bigger gape. Peters took away her brood from a *Haplochromis* mother, and substituted a number of *Tilapia* fry, which closely resemble those of *Haplochromis* and are not much bigger. The foster mother behaved towards the young *Tilapia* just as if they were her own young, and they, on the approach of danger signalled by the mother, swam actively towards her. But they tried to penetrate anywhere on the fore part of her body, at the eye or the gill-cover, and only exceptionally at the mouth, being keyed or adjusted instinctively to seek a much larger object with a larger gape. Their inborn 'schema' of perception apparently includes the size of the normal object.



Response to an image of a certain size and shape is shown by the 'fighting fish' (*Betta splendens*), whose behaviour has been carefully studied by Lissmann (1932). The males fight vigorously with one another, and three stages can be distinguished in their combats. In the first, the males approach with fins spread wide and gill covers open; in the second they swim side by side and strike with their tails; in the third stage they actively attack and bite one another. Lissmann has shown that any object or picture of very approximately the size and shape of *Betta* will elicit stage one of the fight and sometimes stage two. Thus a very rough plasticine model, and other fish of approximately the same size though of different species, will induce the male to approach in fighting guise. The object or image must not be too big, otherwise flight sets in: it must not be too small, or it may be treated as possible food. It need only roughly resemble in size and shape the adequate object, and colour is unimportant. The real fighting movements of stage three are, however, not induced by models or pictures, but only by mirror images or by a living male, and the reason for this is that the real stimulus leading to stage three is the behaviour of the opposing male—the fact that it fights back, or, in the mirror, appears to fight back. The response of the fish to its own movements in the mirror can easily be paralleled in other animals. We have all seen a young pup (and sometimes a grown dog) bark furiously at its own moving image reflected in glass, and even seek the adversary behind the glass. Ritter and Benson (1934) have described how a male Towhee (*Pipilo fuscus petulans*) persistently fought its mirror image in a window-pane day after day, causing the onlookers to enquire 'Is the poor bird demented?' It apparently took its own image for a rival trespassing in its territory.

That the image to which the animal is instinctively predisposed to respond may be a rather ill-defined and generalized one—as is the case in the preliminary fighting of *Betta*—is demonstrated by some interesting observations by Lorenz, carried out on a colony of Jackdaws (*Corvus monedula*) which breed on the roof of his house. I take the following account from Tinbergen (1939). 'If a predator takes a jackdaw, the bird that happens to see it utters a "danger-cry", and at this signal all members of the group hurry to the daw and join in a communal attack. Although a jackdaw has excellent eyes and, in fact, is capable of recognizing each of its companions individually (a surprising faculty!), the alarm-call is a reaction to only a few elements of the predator situation. Lorenz, when carrying a black bathing-suit in his hand, evoked the same reaction. This and other accidental experiments proved that "somebody carrying something black" was all that was necessary to give a response' (p. 23). As Tinbergen points out, this very generalized perception is in normal circumstances sufficiently adequate, since in the vicinity of a jackdaw colony 'somebody carrying something black' will usually be a predator carrying a jackdaw.

In the paper from which I have quoted, Tinbergen also refers to some significant experiments carried out by Lorenz and himself on the response of ducklings and other birds to moving cardboard shapes pulled along a rope slung high above them. The ducklings showed typical fear and escape reactions to any kind of shape moving along above them; other kinds, such as young turkeys, showed these responses only if the model



roughly resembled a hawk, i.e., had a short neck and a long tail. The same shape towed backwards, that is, with the long 'tail' in front, simulating a long neck, and suggesting a goose in flight, was treated as harmless.

According to Hudson (1910), starlings can distinguish between the kestrel and the sparrowhawk, taking no notice of the former, but seeking refuge at once if the latter appears. It is possible that they distinguish the two by their different lengths of tail, and that the birds in Lorenz's experiment were responding to a generalized scheme of sparrowhawk rather than hawk in general.

Turning now to the auditory field, we note that many cases are known where a specific sound is a sufficient and normally adequate perceptual sign. In the field cricket (*Liogryllus campestris*) the chirping sound made by the males through rubbing their wing-covers together suffices to attract the females to them, even though the males be out of sight (Regen, 1924; Baier, 1930). When cages containing respectively males and females of this species were connected by telephone, the females were attracted to and clustered round the transmitter from which the sounds of chirping issued. They paid no attention to a chirping male confined under glass.

In birds, parent-offspring relations are often governed by specific call-notes, danger-notes, and distress-notes, which by themselves are quite sufficient to elicit the appropriate response. Here are three simple examples.

Young rheas, when newly hatched, have no fear of man, and will even, in captivity, adopt him as a substitute parent, as Hudson discovered when he brought up a brood. 'They would follow me about', he tells us, 'as if they took me for their parent; and, whenever I imitated the loud snorting or rasping warning-call emitted by the old bird in moments of danger, they would rush to me in the greatest terror, though no animal was in sight, and, squatting at my feet, endeavour to conceal themselves by thrusting their heads and long necks up my trousers' (1912, pp. 85-6).

Beebe (1925), who experimented with the day old chick of the tinamou, *Crypturus variegatus*, found that it would run to him and crouch beside his foot if he imitated exactly the call-note of the mother. In both these cases, one valent characteristic of the mother elicits the normal response, as to the normal mother.

If a chick is tethered to a small stake it struggles to escape and utters its distress-note; even if it is out of sight behind a board the mother hen will find it and attack the imaginary enemy which is harming it; but if the struggling chick is confined under a glass dish in full sight of the hen, she pays no attention to it, for she cannot hear the distress-note (J. von Uexküll and Kriszat, 1934, p. 52, after Katz). Here the single valent characteristic eliciting protective behaviour on the part of the hen is the distress-note of the chick.

An interesting observation by Lorenz (1935, p. 142) also demonstrates the importance of the distress-note. He tells us that a mallard female with ducklings of her own will come to the assistance of a duckling of another species (*Cairina moschata*) that is calling for help. But when she comes close and sees that it has not the coloration on head and back

of her own ducklings, she attacks and kills it, treating it as 'strange thing near my ducklings'. The distress note gives it 'to-be-protected valence': the wrong markings when perceived change this into 'enemy valence.'

According to Wood Jones and Porteus (1929) the sound of dropping water is one of the very few sensory impressions that will rouse the Blind Worm (*Anguis fragilis*) to activity, and that is because rain normally heralds the appearance of the small grey slugs on which the Blind Worm feeds. 'None of the customary noises of a busy laboratory', they write, 'affect *Anguis fragilis* in the least; intentional efforts at producing a wide range of sounds meet with little better success. The creature does not hear them. They are of no importance and have no meaning to the animal. But let the tap drip, or allow water to drop from the rose of a watering-can, or arrange for an open window as the first few drops of a shower fall, and all is activity with the Blind Worm . . . . Rain drops with their subtle little sounds of falling upon the turf, constitute a biologically relevant auditory stimulus for *Anguis fragilis* . . . . The drops of rain tell the Blind Worm that the little grey slug will be abroad' (pp. 53, 54). They report also that the sound of rain falling is a potent auditory stimulus for many amphibia and reptiles inhabiting the more arid regions of Australia.

In all these cases the response is, of course, not to a valent characteristic of the food-object itself but to an occurrence, the sound of fall of rain, which signifies the probable presence of food. The animal responds to a valent characteristic of the first element in the normal sequence, rain—food.

Certain animals, such as the medicinal leech (*Hirudo*), bugs, mosquitoes and lice, which suck the blood of avian or mammalian hosts, appear to be attracted to their prey, when close to it, mainly by the heat which it gives off. The medicinal leech, which when adult attaches itself only to warm-blooded hosts, will approach and investigate a heated tube, even when it is only 3° C. warmer than the surrounding water (van Baal, 1928). Other species of leech, which do not attack warm-blooded animals, do not show this temperature response.

The common bed-bug (*Cimex lectularis*) is guided towards its host mainly by temperature sense (Rivnay, 1932). It can be excited to movement by holding near it a heated test tube; it directs its antennæ towards the source of heat and approaches it with outstretched proboscis, ready for feeding. It will follow a heated needle about, but pays no attention to a cold one. It responds to the heat of the human body a few centimetres away.

Similar behaviour is shown by the blood-sucking bug *Rhodnius prolixus*, studied by Wigglesworth and Gillett (1934). It is roused to attention by the proximity of a heated tube; erecting its antennæ, and cleaning them with its fore-legs, it then wags them independently, in semaphore fashion, and advances straight towards the tube. 'As soon as one or both antennæ touch the tube, the proboscis is extended and pressed vigorously against its surface.' The response is given nearly as well when the insect is blinded, but it does not occur if both antennæ are removed. The response is to the warm air diffused from the heated body. Smell plays a small part in the finding of the host. It is possible that

vision and perception of vibration are also concerned to some slight extent, for the antennoless insect will actively follow any small moving object and attempt to probe it with the proboscis; it may sometimes be induced to probe whatever it is resting upon if this is lightly tapped. The intact insect will occasionally respond positively to a moving object.

According to Howlett (1910) the females of several kinds of mosquitoes are attracted by heated air currents, and not by the smell of blood or perspiration. His method of experiment was to confine a number in a gauze bag and bring near it a tube containing hot water. 'As soon as the hot air from the tube reached the insects they became restless and began to congregate on the part of the net nearest the tube; as this was brought nearer they became more excited, stabbing with their proboscides through the meshes of the net and displaying the utmost eagerness in their fruitless efforts to puncture the glass.' They tend to hover in the column of heated air ascending from any warm body, such as a hot tea-pot or the human head. The males, which do not suck, show no reaction to heated bodies. As a temperature difference is a necessary condition of the response, this probably explains why in hot climates mosquitoes attack mostly at dark or in the night, whereas in cold climates they may be active at any time.

The biting fly, *Stomoxys calcitrans*, is attracted to its victim, which may be horse or dog, buffalo or man, both by heat and by the smell of the skin; both these valent characteristics elicit approach, the stretching forth of the proboscis and piercing movements. Contact with blood brings out the sucking response, presumably through the sense of taste (Krijgsman, 1930 a). Similar results were obtained with the fly *Lyperosia exigua* (1930 b).

Howlett (1917) observed a response to heat in the common louse (*Pediculus humanus*), the biological object of which is presumably to ensure dispersal to new hosts. A glass tube, containing water at 35–50° C., brought within an inch or two of a louse stimulates it to activity. 'It moves in the general direction of the tube, and in doing so displays a frantic eagerness of movement which is not only amusing but quite foreign to its ordinary method of locomotion. If the tube is brought near a louse which is in the act of feeding, it may show some excitement, but does not ordinarily relinquish its hold' (p. 188). So, too, the louse *Phthirus pubis* responds actively to a heated tube and makes wild efforts to reach it, though if it is feeding it pays little attention to it.

Nuttall also (1917) has observed the positive response of *Pediculus humanus* to a source of warmth, when hungry. If a number are placed on a cloth and the hand moved above them about 2 cm. away, they will follow the hand about.

Temperature response in the human louse is concerned also with finding and remaining in the ecological norm, which is the inner side of the clothing in contact with the warm skin. As Wigglesworth has shown (1941), the preferred temperature, in which the lice collect, is 28–31° C., and this is the normal temperature that obtains between the clothing and the skin.

[For further references to heat as a 'token stimulus' and to preferred temperatures the discussion in Fraenkel and Gunn (1940, chapter xiv.), may be consulted.]



For certain Boas—those provided with labial pits—a warm moving object has food valence. As Noble and Schmidt (1937) have shown, both young and adult specimens of *Boa hortulana* will discriminate between a hot and a cold electric bulb swung past them at a rate of about 40 times a minute. Especially if blindfolded, they will strike only at the warm bulb, up to a distance of 25 cm. or even more, responding to a temperature difference of 0.2° C. or less. Warmth without movement evokes no strike from the blindfolded boa. If the bulbs are swung too rapidly near the snake they elicit an escape or fear response—they acquire danger valence. Species of *Boa* without labial pits do not show the positive response to a warm moving object, and direct experimental evidence demonstrates that these pits are the thermoreceptors concerned.

The 'pit vipers' or Crotalidæ of America, which include the rattle-snakes, also show, when blindfolded, the same discrimination towards the warm bulb as the boas with labial pits, but they will sometimes strike at a cold object waved in front of them. The temperature receptor is the facial pit, which is more highly developed than the labial pits of Boidæ, possessing a membrane which serves to detect air movements. Many Crotalid snakes are crepuscular or nocturnal, and their temperature sense enables them to strike at warm-blooded prey in dim light or darkness. Vision and to some extent smell are also important in food finding, but in the absence of vision the labial pits of Boidæ and the facial pits of Crotalidæ are the most important sensory mechanisms for directing the strike towards warm blooded prey (Noble and Schmidt, p. 287).

As we saw last year, when considering host selection by parasitic Hymenoptera, a specific smell may be extremely important as a sensory sign of the adequate biological object. Here are a few more examples.

First the story of the tick (*Ixodes ricinus*) as it is given by Schulze (1933) and J. von Uexküll and Kriszat (1934). When the female is full grown and inseminated she climbs to the end of an overhanging shoot, and there waits with outstretched fore feet for days or weeks until some small mammal passes beneath her, or some larger one brushes against her. It is the faint smell of butyric acid, given off by the sebaceous glands of the prospective host, and perceived through sense organs situated in the fore feet, that causes her to let go her hold and drop on the host, and it is the warmth of the host that induces her to suck its blood, after she has sought out a relatively hairless spot. If the olfactory organs are removed she will suck all sorts of fluids through a cellophane membrane, provided that they are of the right temperature. Smell, therefore, plays a very important rôle in her life, together with temperature. The host to her is merely something with a specific smell, a certain temperature—and degrees of hairiness.

Krijgsman (1937) gives a somewhat similar picture of the behaviour of young ticks of the genera *Boophilus* and *Rhipicephalus*. About four days after hatching they begin to respond actively to light and climb up grass stems, there to await their host. They are roused to activity by vibratory stimuli, such as are caused by its approach, and attracted to the host especially by the scent of its skin, preferring the skin-smell of horses and cattle to that of man.

Lice also appear to have a preference for the smell of their own particular kind of host. The human louse, for instance, which is rarely found except



on man, 'prefers cloth that has been in contact with human skin to clean cloth or cloth smelling of dog or rabbit. The smell of other lice and of their excreta is also attractive' (Wigglesworth, 1941, p. 106). The same author cites Weber (1929) for the statement that the pig louse (*Haematopinus*) responds to a finger in preference to a glass rod 'and will choose a pig before a dog or a warm oven'—specific smell is important.

For the Scarabaeid beetles, the smell of dung has high food valence. Our common *Geotrupes* finds the dung on which it feeds entirely by smell and not by sight (Warnke, 1931). It scents the breeze with spread antennæ, the lamellæ being held wide apart; if a whiff of dung reaches it, it searches in the general direction of the smell. When to leeward of the dung it may scent it when 4 metres off; if to windward it must be within about 50 cm. When in its searching it comes close to the food, the maxillary palps seem to help in the finding of it. Warnke found that ammonia, skatol and indol, in that order, have a similar attraction to that exercised by dung, of which they are of course constituents.

Some very interesting observations have been made by Heymons and v. Lengerken (1929) on the behaviour of *Scarabaeus* with respect to the pill of dung which it fabricates and buries for consumption. Like *Geotrupes*, it finds the dung by smell, by means of its antennæ and, when close, its maxillary palps. Normally the pill is made of sheep or cow dung and is rolled off, backwards, to be buried in a suitable spot. Experiments showed that the pill is recognized solely by its smell—that and size are its only valent characteristics, not its shape or consistency. Thus little balls of dried *Posidonia* (a marine plant) are accepted if they carry a small smear of fresh dung. Sometimes the beetle trundling such a ball may stop and examine it, but when it comes across the smear of dung it carries on with its rolling. Little balls of lead wrapped up in cloth will also be used if they have been smeared with dung, though they are difficult to roll. The substitute pills need not be spherical to be accepted, provided they smell of dung. A chestnut which had been in contact with dung was rolled away, with some difficulty, and buried, and little bits of wood were treated in the same way, though almost impossible to roll; sometimes the beetle pushed these with its head as an alternative to trundling them along with its feet.

The 'green bottle' fly (*Lucilia sericata*) has acquired notoriety by its habit of ovipositing on sheep, and much work has been done in recent years with a view to reducing these dangerous attacks. The researches of Hobson (1935, 1936) and others have shown that the chief valent characteristic that attracts the gravid female fly to the sheep is the smell of putrefying substances in the fleece, due principally to the presence of indol, skatol and ammonium carbonate; such conditions arise when, for instance, the fleece is contaminated by urine or faeces or the discharge from a wound or sore; moisture is essential for the development of the maggots. It is interesting to note that these flies deposit their eggs also upon carrion, and this is, according to Ritchie (1940), probably the more usual and natural procedure. The feature common to both oviposition sites is no doubt the smell of the products of putrefaction.

Many insects that feed on plants restrict their attacks to one particular species or to a group of allied species. This is well shown, for example,

by lepidopterous larvae, many of which are in this sense 'monophagous'. The cinnabar moth, for instance (*Hipocrita jacobaeus*), feeds almost exclusively on ragwort (*Senecio*). There is some evidence that the specific food-plants are selected by taste, aided perhaps by short range smell, associated with particular chemical compounds.

This has been demonstrated in certain insects by Verschaffelt, an account of whose work I quote from Imms (1934). Verschaffelt (1910) has shown that the larval food-plants of *Pieris rapae* and *P. brassicae* contain a group of glucosides—the mustard oils. He took a solution of sinigrin, which is present in black mustard, and uniformly distributed it over the leaves of plants which the *Pieris* larvae had previously refused to eat. Leaves so treated were readily devoured, and from such experiments it appears that these larvae exhibit strong chemotropism towards mustard oils whose presence in the leaves of certain plants determines the selection of the latter by the larvae for their food. By a similar method of research Verschaffelt has shown that larvae of the sawfly (*Priophorus* (*Cladius*) *padi*), which feed on certain of the Rosaceae, are attracted by the glucoside amygdalin' (p. 75).

The marine gastropod (*Buccinum undatum* L.), like many others, finds its food mainly by smell, the receptor organ being the osphradium, which lies in the mantle cavity near the origin of the siphon. Into the siphon there passes a slow current of water which washes over the osphradium, but this current is very feeble, and sucks water from only about  $\frac{1}{2}$  cm. away.

Its behaviour both in still and in moving water has been carefully studied by Brock (1936). A *Buccinum* at rest in a quiet aquarium is usually withdrawn into its shell, with only the siphon showing. If we place a piece of food on the bottom about 20 cm. away, its juices gradually diffuse out and in time reach the whelk. In water of about 18° C. it reacts in 20 mins.; the siphon is suddenly exerted and set in motion, the head and foot appear, the tentacles are stretched out and begin testing the bottom; the animal is in a state of excitation or attention. In about a minute the animal starts to move; the siphon carries out regular swinging movements from side to side as the whelk creeps in a winding and irregular path towards the food, which it reaches in a few minutes. The testing, probing action of the siphon is the means by which the animal finds the food.

In moving water—which is normal in natural conditions—food-finding by smell is facilitated by positive 'rheotropism'. But the interesting point has been established by Brock that the current must carry food juices before the animal as a whole will respond to it and move upstream; it reacts to a current of pure sea-water with its siphon only, bending this round so that its tip faces the stream. A current of water has therefore a different valence, according as it carries or does not carry chemical traces of food. *Buccinum* cannot, like many decapod crustacea (Brock, 1930, 1939), generate its own respiratory and food-finding current, but its positive response to an externally generated 'food-current' leads normally to the same end-state or result, the finding of the food. The positive response of its siphon to any current facilitates the response of the whole animal to a food-indicating current.

An interesting parallel is afforded by the flat-worm *Planaria alpina*, which, when immature, is generally indifferent to a slow current of water, and may move up or down or across the current. If, however, an immature individual in a weak current is momentarily stimulated by a dilute solution of food extract (*Gammarus*) it responds by becoming positively rheotactic and for 40-60 min. will continue to respond by moving upstream . . . . The stimulus from the food extract can only last for a few seconds, but the animal is instantly aroused and appears excited and reacts positively to the current (Beauchamp, 1937, p. 112). Many dilute chemical solutions will also elicit an upstream movement in weak currents, but the animals react more vigorously to food extract than to anything else of this kind (Beauchamp, 1935, p. 280). A current bearing food-juices has then a very definite food valence, just as in the case of *Buccinum*.

A specific smell may also have danger-valence or sex-valence, as the following examples show. The marine gastropod *Nassa* perceives its enemy the starfish through its chemical sense—one doesn't know whether to call it smell or taste. When pursued and touched by a starfish the snail jerks itself away by a series of zig-zag leaps. This escape-response cannot be elicited by mechanical stimulation but is readily brought about by the secretion from the skins of starfish and sea-urchins (Hoffmann, 1930). A more or less specific 'smell' has in this case danger-valence, as it has also for *Pecten*.

In many Lepidoptera a specific scent or smell diffused from the abdomen of the female may be the sole and normally adequate perceptual sign that directs the male towards her. This is perceived by means of the antennae and sight seems to play little part in sex recognition; the male may be attracted to a box which has once contained a female and is not attracted to a female enclosed in an air-tight glass vessel. The observations of Kellogg (1907) on the silkworm moth (*Bombyx mori*) show the all-powerful nature of this scent attraction. The female ready to pair protrudes a paired scent organ from the last abdominal segment; the male finds her by smell and not by sight, and when he has found her orientates himself for copulation by tactile sense. But if the end of the female's abdomen is cut off before the male finds her he is attracted to the amputated part and tries to pair with it, paying no attention to the mutilated female even if she be close by.

The examples which I have collected together in this address, show us, I think, two things, (1) that the animal is predisposed to attend to and perceive sensory signs of objects and events that are biologically significant to it, and (2) that these signs are often few and simple, and yet in normal circumstances adequate.

As I pointed out last year, predisposition to attend to particular objects and events, or signs of such, which are biologically significant in relation to the animal's special needs and requirements, is one of the essential characteristics of instinctive behaviour. From the psychological standpoint an instinct is defined by McDougall (1936) as 'an inherited or innate psycho-physical disposition which determines its possessor to perceive, and to pay attention to, objects of a certain class, to experience an emotional excitement of a particular quality upon perceiving such an object, and to act in regard to it in a particular manner, or, at least, to experience



an impulse to such action' (p. 25). To which psychological definition we can now add, from the biological point of view, that the 'objects of a certain class' are, usually, objects that are biologically significant for the particular animal concerned, and they are often represented by simple sensory or perceptual signs that are normally adequate. That a particular species or group of species is predisposed or preadapted to attend to particular sensory signs—as the scarab to the smell of dung, or the wolf spider to small moving objects—is simply one facet or aspect of the general fact that each animal species is, after its kind, a functional and ecological specialist, adapted in structure, physiological functioning and behaviour for a particular manner of life, and adapted integrally as one unitary concern.

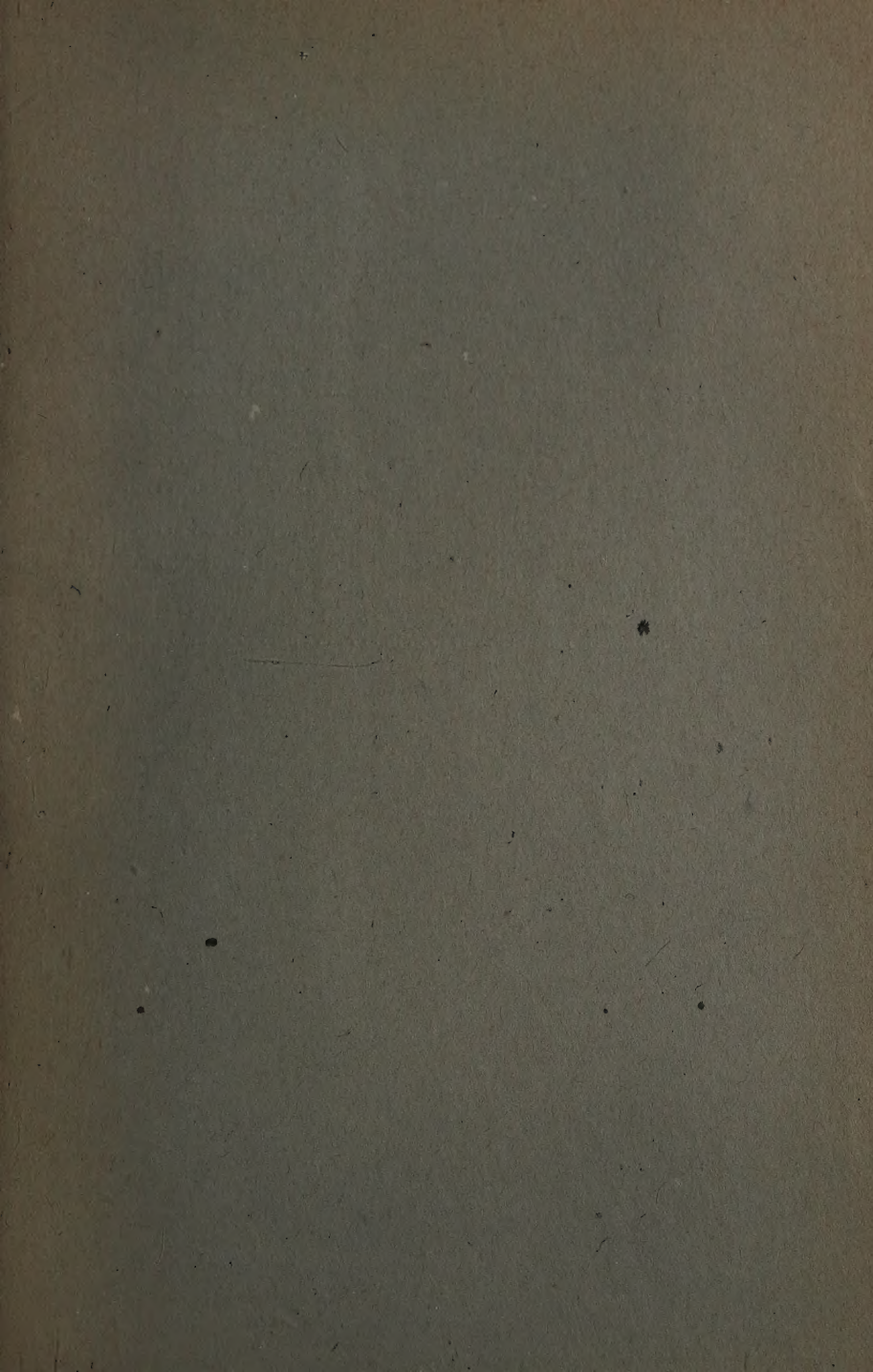
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